14 Assembly of Species Communities

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Summary

This chapter explores the origin of differences in community structure, such as those between different islands of the same archipelago, between different localities on the same island, between different adjacent habitats, and between

different biogeographical regions. The working hypothesis is that, through diffuse competition, the component species of a community are selected, and coadjusted in their niches and abundances, so as to fit with each other and to resist invaders. Observations are derived from bird communities of New Guinea and its satellite islands, of which some are at, some above, and some below equilibrium in species number (*S*).

From exploration of numerous islands with various values of *S*, so-called incidence functions are constructed for individual species. These relate *J*, the incidence of occurrence of a particular species on islands of a certain *S*-class, to *S*. Species are classified according to their incidence functions into six categories: high-*S* species, confined to the most species-rich islands; A-, B-, C-, and D-tramps, present on the most species-rich islands and also on increasing numbers of increasingly more species-poor islands; and supertramps, confined to species-poor islands and absent from species-rich islands. Since different species have incidence functions of different shapes, the fauna of any real island is a very nonrandom subset of the total species pool.

The high-*S* category consists partly of endemic species of forest on large islands, partly of non-endemic species of scarce habitats often unrepresented or barely represented on smaller islands. Tramps, especially C- and D-tramps, are mostly nonendemic species characteristic of habitats that occur on virtually any island.

The dependence of incidence on area involves several factors, which vary from species to species: whether the required habitat of a species occurs on small islands; minimum territory size for species in which each pair maintains an exclusive territory; minimum year-round support area for species dependent on patchy or seasonal food supplies; population size in relation to short-term and long-term population fluctuations; and the role of "hot spots" (areas of locally-high utilizable resource production) in colonization and in recovery from population crashes.

Dispersal ability of species in different incidence categories has been assessed from data sources such as recolonization of islands defaunated by volcanic explosion or tidal wave, long-term records of vagrants, and direct observations of overwater colonization. Especially in the tropics, many bird species capable of strong flight refuse to cross water barriers of even a few miles. Dispersal rates are highest for supertramps and D-tramps, followed by C-tramps, B-tramps, and nonendemic A-tramps of scarce habitats. For high-*S* species, such dispersal as there is may be associated with rare population "blooms."

There is no obvious correlation between clutch size and incidence category. However, supertramps and D- and C-tramps have longer breeding seasons and raise more broods per year than do other species.

Supertramps have extraordinarily catholic and unspecialized habitat preferences, high reproductive potential, and high dispersal ability. They are competitively excluded from species-rich islands by "*K*-selected" species. However, faunas dominated by supertramps maintain population densities up to nine times *higher* than those of K-selected faunas composed of the same number of species. Thus, the supertramp strategy may be contrasted with an inferred overexploitation ethic practised by high-S species, which are selected by competition to harvest early and overexploit. The high-S species thereby reduce resource levels below the point where other species can survive, even though this diminishes the rate of resource production and hence the population density of the harvesting species.

In a few instances, competition expresses itself in "simple" checkerboard distributions, by which species replace each other one-for-one. The frequent occurrence of "empty squares," however, shows that even these cases are complex. In the great majority of species groups or guilds, competitive exclusion involves so-called diffuse competition, i.e., the combined effects of several closely related species. Detailed examination of four guilds reveals the following types of assembly rules for species communities:

If one considers all the combinations that can be formed from a group of related species, only certain ones of these combinations exist in nature.

These permissible combinations resist invaders that would transform them into a forbidden combination.

A combination that is stable on a large or species-rich island may be unstable on a small or species-poor island.

On a small or species-poor island a combination may resist invaders that would be incorporated on a larger or more species-rich island.

Some pairs of species never coexist, either by themselves or as part of a larger combination.

Some pairs of species that form an unstable combination by themselves may form part of a stable larger combination.

Conversely, some combinations that are composed entirely of stable subcombinations are themselves unstable.

The forbidden combinations do not exist in nature because they would transgress one or more of three types of empirical rules: compatibility rules banning the coexistence of certain closely related species under any circumstances; incidence rules, implicit in incidence functions; and combination rules, which cannot be predicted from incidence functions.

Most of the evidence for these assembly rules is drawn from comparison of communities on different islands. However, examples are also drawn from communities at different localities, or in different habitats, or at different altitudes, or at different heights above the ground, on the same island. In some cases one can recognize simple effects of one-to-one competition. In other cases, one can recognize assembly rules describing more complex competitive effects and permitted combinations of several related species. In still more complex cases, competitive effects must be described by incidence functions relating the occurrence or niche limits of one species to diffuse competition from many other species. Thus, recognition of assembly rules may help us understand competitive effects on the spatial niche limits of a given species, and the puzzling tropical phenomenon of patchy distributions.

Much of the explanation for assembly rules has to do with competition for resources and with harvesting of resources by permitted combinations so as to minimize the unutilized resources available to support potential invaders. Communities are assembled through selection of colonists, adjustment of their abundances, and compression of their niches, in part so as to match the combined resource consumption curve of all the colonists to the resource production curve of the island. Members of permitted combinations must also be "companions in starvation"—i.e., must be similar in their tendencies to overexploit and in their tolerances for lowered resource levels, thereby starving less tolerant species off the island. Thus, consumer species form hierarchies with respect to exploitive strategy. The conditions under which overexploitation becomes a useful strategy for its practitioners are examined by loop analysis. Also relevant to the origin of assembly rules are two further factors: dispersal abilities, which permit only certain species to have a high incidence on small islands with high extinction rates; and transition probabilities, i.e., ease of assembling a species combination in one or a few steps from other permitted combinations.

Major unsolved problems include: the development of mathematical models for incidence functions; extensions to habitat communities and to locally patchy communities; the relative roles of chance and of predestination (i.e., detailed matches of different species combinations to slightly different local production curves) in the build-up of alternate communities; and applications to conservation problems.

Introduction

The understanding of alternate, stable, invasion-resistant communities of coadjusted species poses a major current problem in ecology. Sets of such communities occur in similar habitats in different biogeographical regions, in similar habitats on different islands colonized from the same species pool, in similar habitats at different localities on the same large island or continent, and in different adjacent habitats. The theoretical basis for the existence of alternate stable communities was brilliantly explored by Robert MacArthur (1972) in *Geographical Ecology*. A conceptual framework is now available within which field observers can approach such unsolved problems as the following:

To what extent are the component species of a community mutually selected from a larger species pool so as to "fit" with each other?

Does the resulting community resist invasion? If so, how?

To what extent is the final species composition of a community uniquely specified by the properties of the physical environment, and to what extent does it depend on chance events (e.g., the question of which colonists arrive first, possibly also affecting which subsequent arrivals are compatible with the successful first colonists)?

The present chapter discusses such problems in the light of observations on bird communities of New Guinea satellite islands. It will be shown that (a) the probabilities or incidences of occurrence of particular species in a community bear neat empirical relations to the total species number in the community; (b) these so-called incidence functions can be interpreted in terms of island area plus a species' habitat requirements, dispersal ability, birth and death schedule, exploitation strategy, and competitive relations; (c) the various species in a guild can coexist only in certain combinations; (d) these permitted combinations resist invaders that would result in forbidden combinations; and (e) lowering of resource levels by coadjusted constellations of species, to below the point where invaders can survive, may be an important mechanism of competitive exclusion.

Statement of the Problem

The structure of a species community may be described in terms of its species composition, together with the resource utilization, and distribution and abundance in space and time, of each component species. Comparison of different communities at any one of four levels generally reveals some differences in structure:

1. Differing but adjacent habitats differ in community structure, even though there may be no physical barriers preventing species of one habitat from invading another habitat (cf. Cody, Chapter 10).

2. Differences in community structure may exist between similar habitats in different areas of the same continent or large island, or even between similar habitats in areas that are in immediate contact and constitute artificially defined sections of a continuum. This phenomenon is especially marked in the tropics. The result is often that tropical species are patchily distributed with respect to the available habitat. Figures 33–38 will present examples of these baffling distributional patterns.

3. Communities on similar islands colonized from the same species pool may differ. For example, the islands Sakar and Tolokiwa lie 29 miles apart in the Bismarck Sea near New Guinea, differ in area by only 13%, are geologically similar, support similar forest, have derived their birds from the same sources, and support similar numbers of lowland bird species (36 and 40, respectively). Yet Tolokiwa lacks three of the seven most abundant species of Sakar, Sakar lacks eight of the 15 most abundant species of Tolokiwa, and only 23 species are shared. In the Pearl Archipelago off Panama, MacArthur, Diamond, and Karr (1972) cite equally striking differences in bird species composition between Chitre and Contadora islands, which are only 1 mile apart. Furthermore, a species that is shared between similar islands may still occupy different habitats and have different abundances. For example, the fruit pigeon *Ptilinopus insolitus* is present both on Sakar and on Tolokiwa, but on Sakar it is widespread whereas on Tolokiwa it is confined to mid-montane forest. Its congener *Ptilinopus solomonensis* is present both on Sakar and on Tolokiwa and occupies similar habitats on the two islands, but is approximately six times more abundant on Tolokiwa than on Sakar.

4. The examples mentioned so far involve communities formed from the same species pool and lying within the same

biogeographic region or faunal province. Much larger differences are observed between more distant communities lying in different faunal provinces. For more than a century, from the time of Sclater and Wallace until the publication of *The Theory of Island Biogeography* by MacArthur and Wilson (1967), these differences formed the principal subject matter of biogeography. Although similar habitats in South America, Africa, and Australia may share few species in common, these communities may exhibit remarkably detailed convergent similarities in structure (Cody, Chapter 10; Karr and James, Chapter 11). The borders of the world's major faunal provinces are formed by present and past barriers to movement of organisms. These barriers have not served to eliminate colonization, but rather to reduce it to a level where great differences are maintained indefinitely between the communities on opposite sides of the barrier. If the communities did not possess some resistance to invasion, colonization across the barriers for millions of years would have smoothed many of the differences between even the major faunal provinces. Thus, the differences between the Australian Region and the Oriental Region present many of the same problems, albeit in more marked form, as the differences between Sakar and Tolokiwa islands in the Bismarck Sea.

These examples suggest (but do not prove) that the species in a community are somehow selected, and their niches and abundances somehow coadjusted, so that the community possesses some measure of "stability." Stability implies the existence of several different properties, some of which are easier to demonstrate than others. The most obvious thing we mean in describing a community as "stable" is that its present species composition is likely to persist with little change if there is no change in the physical environment. This property is easy to assess by comparing historical surveys with recent surveys. For instance, faunal surveys of a given New Guinea satellite island a century ago and today yield much more similar species compositions than do surveys of several different islands of similar size at the same time. The property of stable species composition suggests the existence of an additional property, namely, ability of a community to resist invasion by new species. This property is more difficult to document, because one needs much more than two faunal surveys at different times. A particular species may be absent from a particular island because the existing community prevents colonizing individuals of the new species from establishing themselves, or merely because colonizing individuals of the species may never reach the island at all. To document resistance to invasion requires sufficiently extensive observations so that arrivals of colonizing individuals, and their failures to establish stable populations, are detected. Finally, the property of resistance to invasion suggests a further property, which is still more difficult to document as well as to formulate, namely, that the existing community utilizes available resources in some optimal manner (MacArthur, 1970; MacArthur, 1972, pp. 231–234).

It seems likely that competition between species plays a key role in the integration of species communities. Real or potential utilization of some of the same resources could be an obvious explanation for why similar species do not occur in the same community, unless their resource utilizations are somehow coadjusted. Numerous recent studies have provided clear-cut distributional evidence for competition between members of a pair of related species. These examples are valuable in documenting the existence of competition, but by themselves they do not account for much of the real world. Far more often, the presence or absence of a given species, and intercommunity variation in its abundance or spatial distribution, cannot be understood predominantly in terms of a correlated distribution of any single other species. It is then a logical extension of simple two-species distributional checkerboards to invoke "diffuse competition"—i.e., the complex situations resulting from the sum of competitive effects from many other somewhat similar species (Diamond, 1970a, p. 530; 1970b, pp. 1716–1717; MacArthur, 1972, pp. 43–46 and 249; Pianka, Chapter 12). The power of this concept is that, in principle, it can explain anything. Its heuristic weakness is that, if it is important at all, its operation is likely to be so complicated that its existence becomes difficult to establish and impossible to refute. Such a concept deserves to be greeted with skepticism until its importance can be documented. A profitable biogeographic approach to documenting diffuse competition would seem to be, first, to seek evidence whether variation in the incidence, niche, or abundance of a given species is correlated with variation in total species number; then, to seek to trace out cases in which the distribution of a given species can be clearly related to the distribution of certain *combinations* of a few other species, yielding patterns that are analogous to two-species distributional checkerboards but more complex.

Such a test of the hypothesis of alternate, stable, invasion-resistant communities integrated by diffuse competition requires a field situation or experimental situation with the following properties: (a) a large number of communities that provide a similar physical environment and habitat structure; (b) a large species pool, varying fractions and combinations of which occur in the available communities; (c) availability of evidence that a species absent from a given community actually has had access, and that its absence is not simply due to a total lack of immigrants; (d) availability of evidence that the community does resist invasion, and that failure of attempted colonizations is not simply due to unsuitable habitat; (e) availability of cases in which a community has been displaced from equilibrium, so that relaxation towards equilibrium can be studied.

The avifauna of New Guinea and its satellite islands provides a favorable test situation. Considerable ecological and evolutionary information exists about the New Guinea species pool of 513 breeding nonmarine bird species. Surrounding New Guinea, and colonized by varying fractions of this species pool, are thousands of islands of varying sizes and at varying distances, providing numerous sets of replicate communities. Ornithological ex-

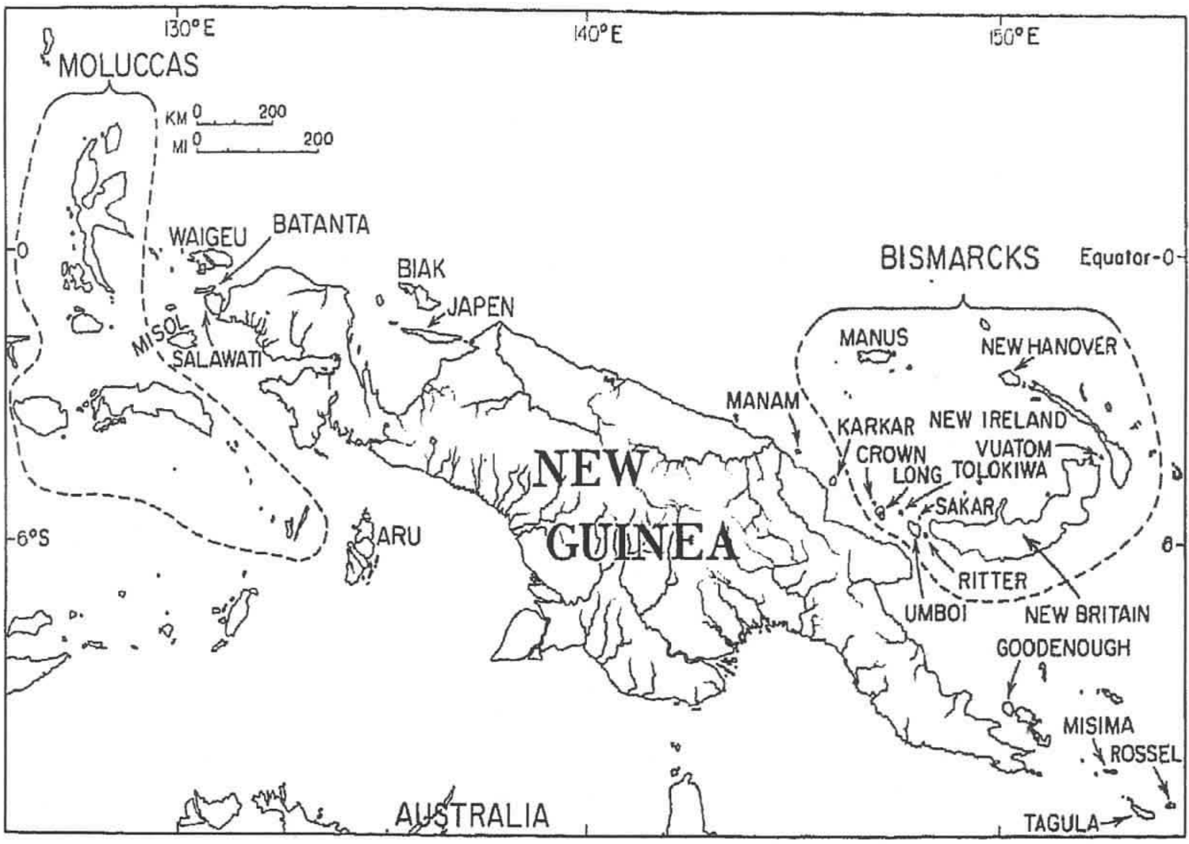


Figure 1 Map of the New Guinea region with names of some of the islands to be discussed.

ploration has been sufficiently intensive to provide not merely species lists but, for some islands, instances of successful and unsuccessful colonizations. Species numbers on some islands have been displaced above what would be their present value at equilibrium by Pleistocene episodes of lowered sea level, which joined some islands to New Guinea, joined other islands to each other, and expanded still other islands in area. Species numbers on other islands have been displaced below equilibrium by Krakatoa-like volcanic explosions or by tidal waves. Some species called supertramps are particularly useful in studying community integration, because of their high colonization rates and sensitivity to competition. We shall see that the distributions of most species can be neatly related to total species number in a community; and that, in a few cases, it is possible to relate species distributions to diffuse competitive effects from specific combinations of related species.

Background: The New Guinea Biogeographic Scene

New Guinea lies near the equator, north of Australia, at the eastern end of the Indonesian Archipelago, and at the faunal gateway to the islands of the southwest Pacific. Figure 1 gives the positions of some of the islands that will be mentioned. The predominant natural vegetation is rainforest, but there are also savannas in low-rainfall regions of south New Guinea, alpine grassland at high elevations on New Guinea and a few of the highest satellite islands, and glaciers above 16,000 feet on the highest peaks of New Guinea's mountain backbone (the so-called central cordillera).

On satellite islands near New Guinea the number of lowland bird species S increases with island area (A, in square miles), approximately according to the empirical relation (Diamond, 1972b)

$$S = 15.1A^{0.22} \qquad (1)$$

Within the satellite archipelagoes, such as the Bismarcks or the New Hebrides, the exponent of area has a lower value (Figures 2, 3). The deviation below a linear $\log S - \log A$ relation at very low A values (Figure 3) is in the direction predicted by May (section 5 of Chapter 4). On mountainous islands each 1000 feet of elevation L is associated with a number of montane species equal to 2.7% of the species number at sea level. S decreases exponentially with distance d from New Guinea, by a factor of 2 for each 1620 miles. Thus, the total number of species on an island is given by the relation

$$S = 15.1(1 + 0.027\ L/1000)(e^{-0.693d/1620})A^{0.22} \qquad (2)$$

On islands within a few miles of a more species-rich island, S is higher than predicted from eq. 2. New Guinea has 513 species, of which 325 are in the lowlands. The most species-rich satellite island, Aru, has 160 lowland species, 49% of the number for New Guinea. At the other extreme, some small or remote islands have only one species.

Species numbers on three types of islands were displaced above the present equilibrium value (predicted from eq. 1) by injection of species during the Pleistocene, at times of lower sea level. One group of present-day islands (points +, Fig. 2) was then connected to New Guinea itself and must have received most of the New Guinea lowlands avifauna. Other islands (points ⊕, Fig. 2) were connected to larger satellite islands, though not to New Guinea itself, and must have received most of the avifauna of these islands. Still other islands (points □, Fig. 2) that lie on large shallow shelves were formerly much larger in area and must formerly have held an equilibrium species number larger than the value appropriate to their present shrunken area. When sea level rose about 10,000 years ago, all these islands must have found themselves supersaturated with bird species in relation to the equilibrium value for their new condition. As shown by Figure 2, species numbers on the smaller of these islands have already relaxed to the equilibrium value given by eq. 1, whereas the larger of these islands are still "supersaturated." Salawati, for example, has 134 lowland species, considerably less than the New Guinea total of 325, most of which it must have supported at times of lower sea-level up to about 10,000 years ago, but still more

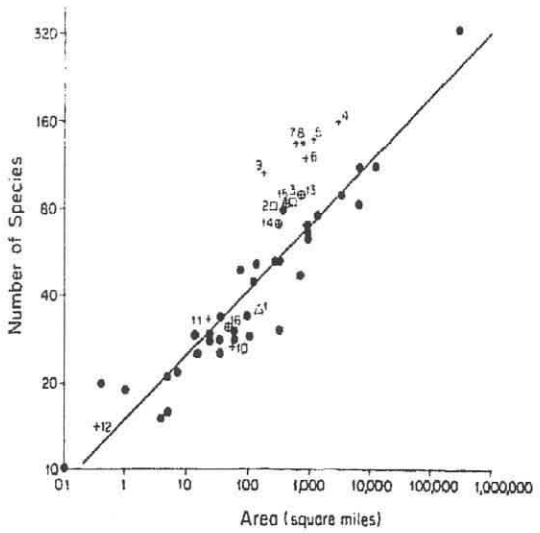


Figure 2 Number of resident land and fresh-water bird species on New Guinea satellite islands, plotted as a function of island area on a log-log scale. ●, islands on which species number is presumed to be at equilibrium. The avifaunas of the remaining, numbered islands are in various stages of "relaxation" after displacement of species number from an equilibrium value. △, exploded volcanoes: 1 = Long. □, contracted islands: 2 = Goodenough, 3 = Fergusson. ⊕, islands formerly connected by land bridges ("first-order bridges") to New Guinea itself: 4 = Aru, 5 = Waigeu, 6 = Japen, 7 = Salawati, 8 = Misol, 9 = Batanta, 10 = Pulu Adi, 11 = Ron, 12 = Schildpad. +, islands formerly connected by land bridges ("second-order bridges") to some larger island but not to New Guinea itself: 13 = Batjan, 14 = Amboina, 15 = New Hanover, 16 = Tidore. The straight line is eq. 1 ($S = 15.1A^{0.22}$), the least-mean-squares fit to all points except the first-order land-bridge islands. Note that large land-bridge islands and contracted islands deviate in the direction of an excess of species, that small islands do not, and that the deviation is more marked for the first-order land-bridge islands or contracted islands. (From Diamond, 1972b.)

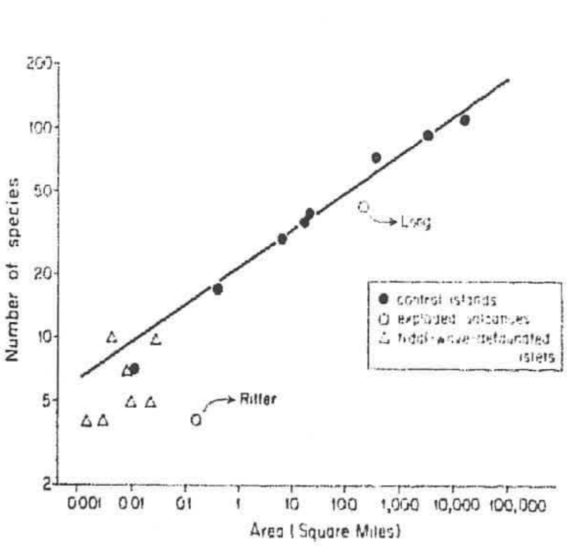


Figure 3 Number of resident, nonmarine, lowland bird species S on New Britain and neighboring islands in the Bismarck Archipelago, plotted as a function of island area on a double logarithmic scale. Symbols: ●, relatively undisturbed "control" islands (from left to right, Midi, Malai, Crown, Sakar. Tolokiwa, Umboi, New Ireland, New Britain); ○, exploded volcanoes; △, coral islets inundated by the Ritter tidal wave in 1888. The straight line $S = 22.4A^{0.18}$ was fitted by least-mean-squares through points for the seven larger control islands. Species number is still below equilibrium on the two exploded volcanoes, especially on Ritter, because of incomplete regeneration of vegetation. The scatter in S values for the smallest islets, and their general deviation below the line for larger control islands, is attributed to their very low S values and few individuals per species (cf. Table 4), and is in the direction predicted by May (section 5 of Chapter 4). (After Diamond, 1974.)

than double the number of 62 predicted at equilibrium for its area from eq. 1. Calculated exponential time constants or "relaxation times" for relaxation of species number to equilibrium are around 6,000–18,000 years for the largest satellite islands ($A = 300$–$3{,}000$ sq. mi.). That is, larger islands remain supersaturated for much longer than do smaller islands (Diamond, 1972b). Cody (Chapter 10, Figure 11) has discovered a similar relaxation effect in a continental avifauna. On the small island of Barro Colorado, which was part of the Panama mainland until about 1914, the relaxation time of the avifauna is short enough for decreases in species number to have been detectable each decade (Wilson and Willis, Chapter 18; Willis, 1974; see also Terborgh, 1974a, 1974b).

Species numbers on three other types of islands have been displaced below, rather than above, the equilibrium value. First, Long and Ritter were defaunated in historical times by cataclysmic, Krakatoa-like volcanic explosions (Diamond, 1974). The species number on Ritter, which exploded in 1888, is still 75% below the equilibrium value (Figure 3). Lowland species number on Long, which exploded about two centuries ago, is 25% below the equilibrium value and has remained "stuck" in this depressed quasi-steady state for at least the last 40 years. These bird species deficits on Ritter and Long are clearly attributable to the stunted, subclimax, lowland forest on both islands; lowland bird species number must have equilibrated rapidly with the available vegetation. In the mountains of Long, however, where the forest is already structurally mature, there is a large deficit of montane bird species that cannot be attributed to stunted vegetation and that indicates much slower dispersal by montane species than by lowland species, as already assumed by ornithologists for other reasons (Stresemann, 1939; Mayr, 1942). A second group of defaunated islands consists of seven coral islets defaunated by a tidal wave in 1888. All now support a climax forest and an equilibrium number of bird species. Finally, on one very small islet (3 acres) at a distance of 2 miles from New Guinea, I carried out experiments in removing existing bird populations and observing recolonization. Equilibration was apparently complete in less than two days and occurred at an initial rate of one colonizing species arriving per hour.

For three satellite islands much larger than this experimentally defaunated islet, estimates have been obtained of the rates at which bird species "turn over" at equilibrium, by natural immigration and extinction. On Karkar, for which surveys are available for the years 1914 and 1969, the estimated average turnover rate for the intervening years is 0.32%/year (Diamond, 1971). That is, during each decade a number of established species equal to 3.2% of the total bird species number disappeared, and an approximately equal number of immigrants successfully established breeding populations. For Vuatom, the turnover rate between 1906 and 1930 is 0.40%/year. The rate for Long, measured not at equilibrium but in the quasi-steady state that has persisted at least from 1933 to 1972, is 0.18%/year. These turnover rates are comparable to values calculated for the California Channel Islands (Diamond, 1969; Jones and Diamond, 1975) and for Mona in the Caribbean (Terborgh and Faaborg, 1973).

Incidence Functions

If one examines the detailed distributions of numerous individual species in the New Guinea region, several types of patterns emerge. Certain species are found only on the largest, most species-rich islands. At the other extreme, certain species occur only on the smallest or most remote, most species-poor islands. There is a whole spectrum of intermediate cases. These general impressions can be quantified and depicted for each species by the type of graph illustrated in Figures 4-15, which we shall term an incidence function of the species. Such a graph can serve as a "fingerprint" of the distributional strategy of a species, once the forms that the graph may assume have been interpreted.

Incidence functions are constructed by grouping well-surveyed islands together into classes, the islands in each class sharing a similar total number of species. One class, for example, may be defined as consisting of islands with 4-6 species, another of islands with 7-10 species, another of islands with 11-20 species, etc. Construction of such functions is practical only if there are a large number of well-surveyed islands, permitting arbitrary definition of classes, each spanning a narrow range of total species number. For a given species, one calculates the incidence of occurrence on islands of a given class—i.e., the fraction of the class's islands on which the species actually occurs. Incidence of occurrence of the given species, J, is then plotted against the average total number of species S in each island class. Sufficient information is available to construct sets of functions for the avifaunas of half-a-dozen archipelagoes of the New Guinea region and southwest Pacific.

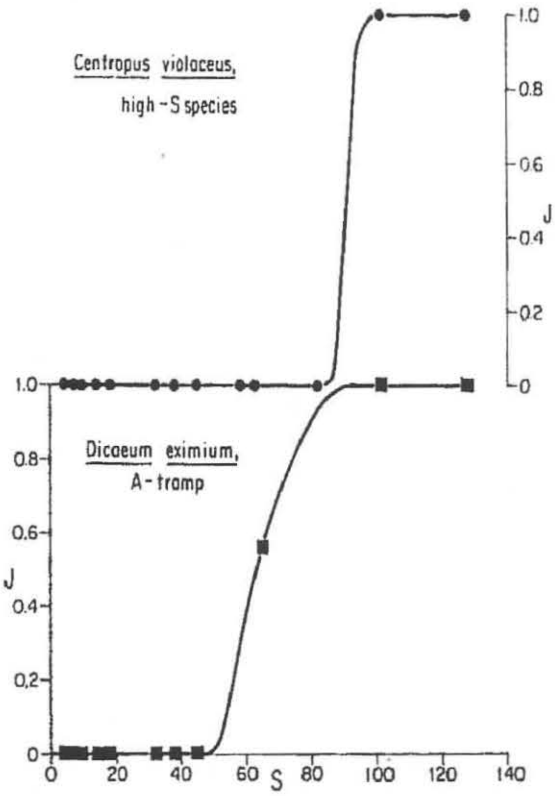


Figure 4 Above, incidence function for the high-S cuckoo *Centropus violaceus* in the Bismarck Archipelago, identical to the function for several other high-S species (the plover *Charadrius dubius*, the pigeon *Gymnophaps albertisii*, the parrot *Micropsitta bruijnii*, the wood swallow *Artamus insignis*). Below, incidence function for the A-tramp berrypecker *Dicaeum eximium*. To construct Figure 4-15, islands of the Bismarck Archipelago were divided into groups such that value of the total species number S of all islands in a given group fell within a narrow range ΔS. ΔS was generally ≤ 3 for $S < 20$, 2-10 for $20 < S < 65$, and 2-20 for $S > 65$. The ordinate J is the incidence of the given species (i.e., the fraction of the islands in the group on which the species occurs), and the abscissa S is the average species number for the islands of the group. Thus, $J = 1.0$ or $J = 0$ means that a species occurs on all islands or on no island, respectively, that has approximately the indicated species number. Each point is usually based on 3-13 islands, except that the two-right-most points usually represent one island each ($S = 101$ and 127).

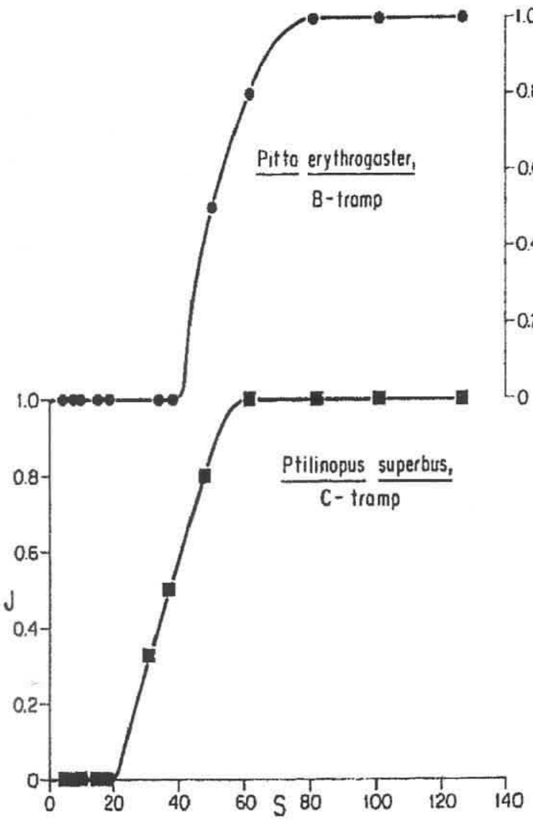


Figure 5 Incidence functions for the B-tramp pitta *Pitta erythrogaster* (above), and for the C-tramp pigeon *Ptilinopus superbus* (below), in the Bismarcks.

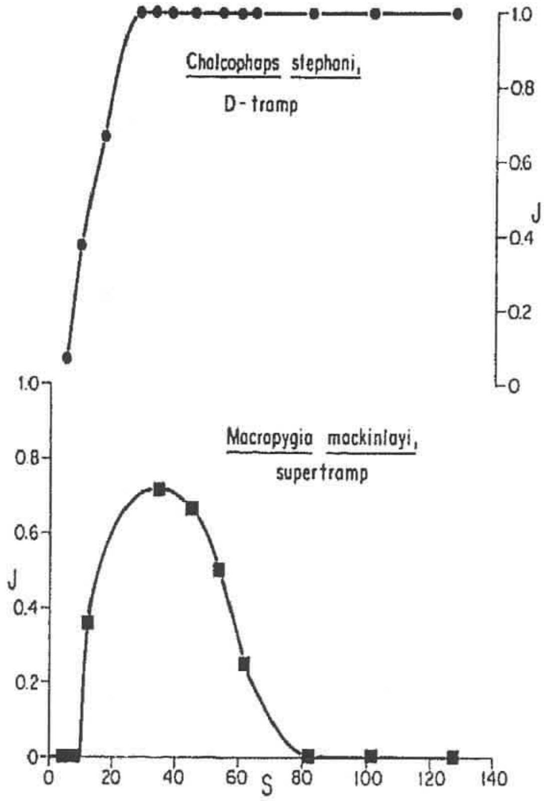


Figure 6 Incidence functions for the D-tramp pigeon *Chalcophaps stephani* (above), and for the supertramp pigeon *Macropygia mackinlayi* (below), in the Bismarcks.

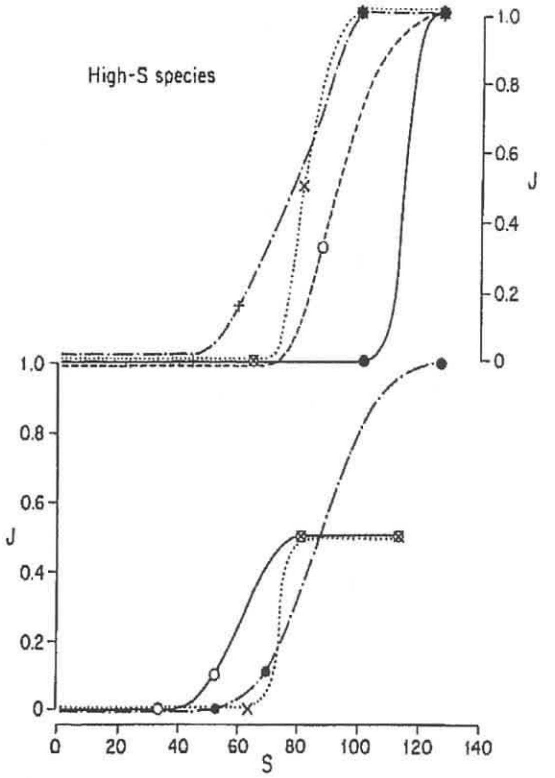


Figure 7 Incidence functions for various high-S species in the Bismarcks. Above, points ● and line –, the rail *Rallus insignis,* hawks *Accipiter brachyurus* and *Milvus migrans,* kingfisher *Halcyon albonotata,* parrot *Cacatua galerita,* owl *Tyto aurantia,* warbler *Ortygocichla rubiginosa,* flycatcher *Monachella muelleriana,* honeyeater *Melidectes whitemanensis,* finch *Lonchura melaena,* and several other species. Points O and line – – –, the ducks *Dendrocygna guttata* and *D. arcuata,* heron *Egretta intermedia,* and honeyeater *Myzomela cineracea.* Points X and line · · · ·, the pigeon *Ducula finschii,* parrot *Vini rubrigularis,* and hornbill *Aceros plicatus.* Points + and line – · – · –, the pigeon *Columba pallidiceps* and cuckoo-shrike *Coracina lineata.* Below, points ● and line – · – · –, the hawk *Henicopernis longicauda* and button-quail *Turnix maculosa.* Points O and line –, the rail *Rallina tricolor.* Points X and line · · · ·, the heron *Butorides striatus.* Most $J = 0$ points are omitted for clarity.

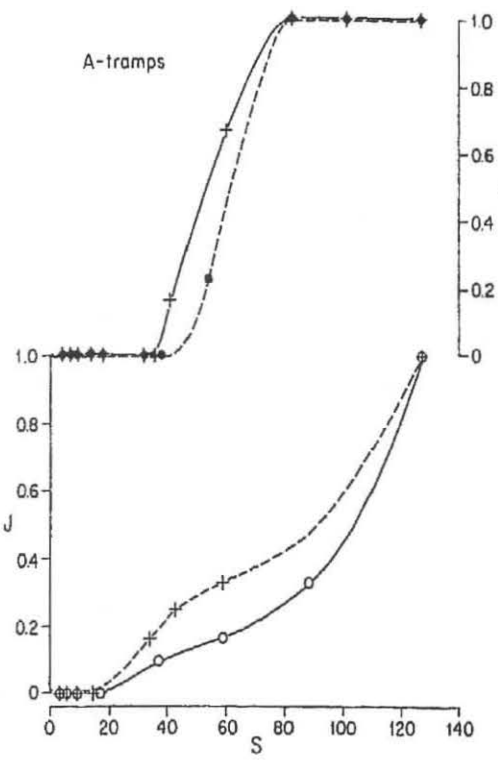


Figure 8 Incidence functions for various A-tramps in the Bismarcks. Above, points + and line —, the pigeon *Ptilinopus rivoli*, parrot *Geoffroyus heteroclitus*, and kingfisher *Ceyx lepidus*. Points ● and line — — —, the white-eye *Zosterops hypoxantha*. Below, points O and line —, the bee-eater *Merops philippinus*. Points + and line — — —, the rail *Porphyrio porphyrio*.

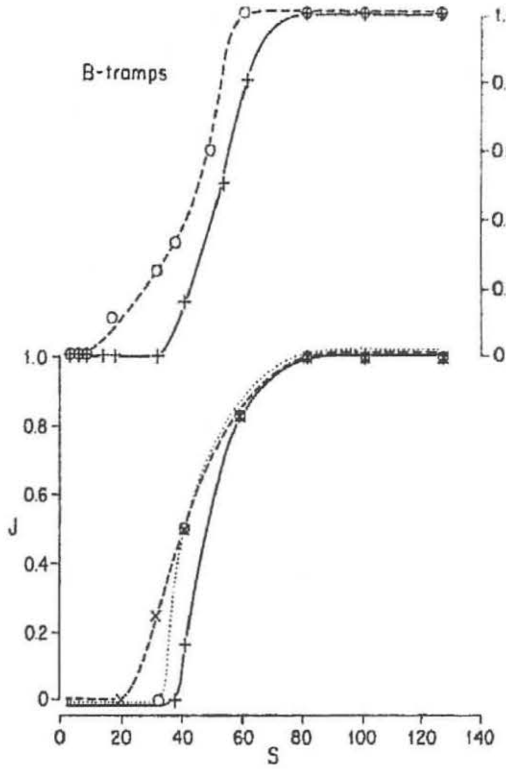


Figure 9 Incidence functions for various B-tramps in the Bismarcks. Above, points + and line —, the grass warbler *Cisticola exilis*. Points O and line — — —, the cuckoo *Cacomantis variolosus*. Below, points X and line — — —, the rail *Amaurornis olivaceus*. Points O and line · · · ·, the pigeon *Ducula rubricera*. Points + and line —, the nightjar *Caprimulgus macrurus*.

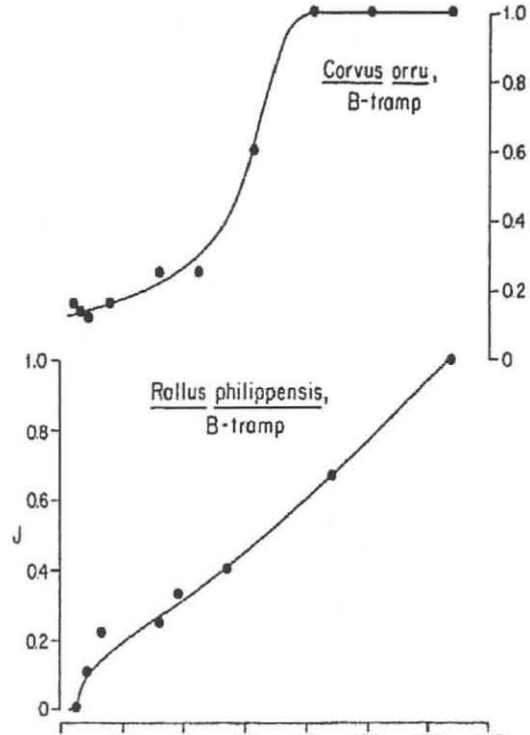


Figure 10 Incidence functions for two B-tramps in the Bismarcks. Above, the crow *Corvus orru*. Below, the rail *Rallus philippensis*.

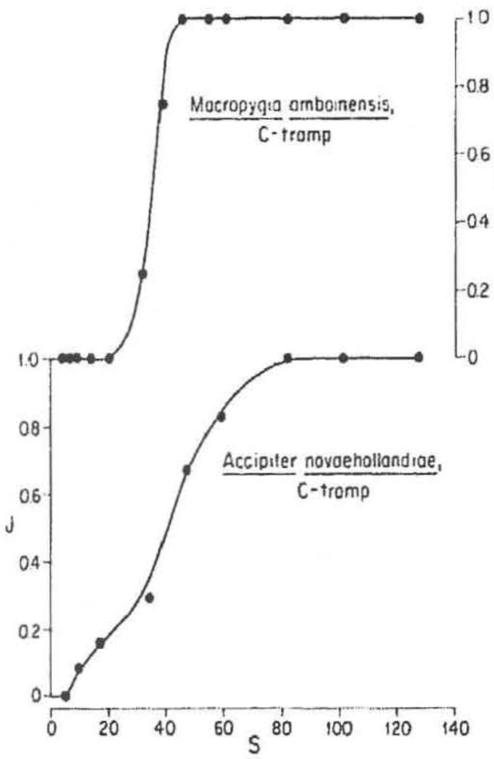


Figure 11 Incidence functions for two C-tramps in the Bismarcks. Above, the pigeon *Macropygia amboinensis*. Below, the hawk *Accipiter novaehollandiae*.

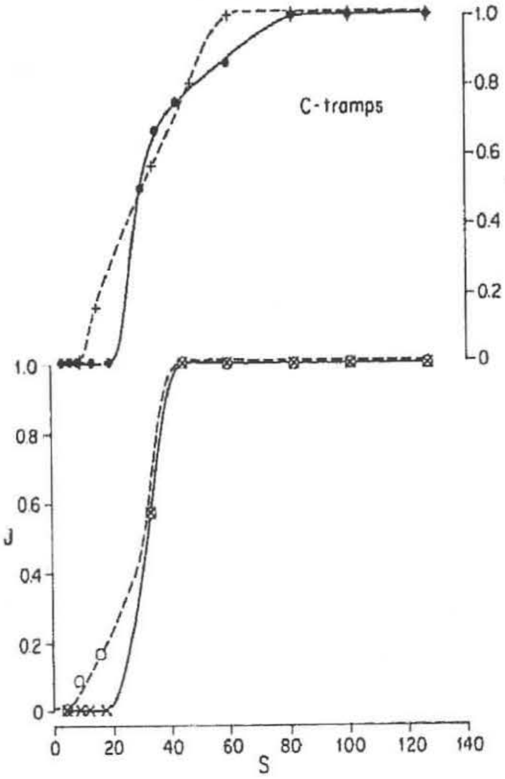


Figure 12 Incidence functions for various C-tramps in the Bismarcks. Above, points ● and line —, the cuckoo-shrike *Coracina tenuirostris*. Points + and line – – –, the parrot *Micropsitta pusio*. Below, points X and line —, the kingfisher *Alcedo atthis*. Points ○ and line – – –, the heron *Nycticorax caledonicus*.

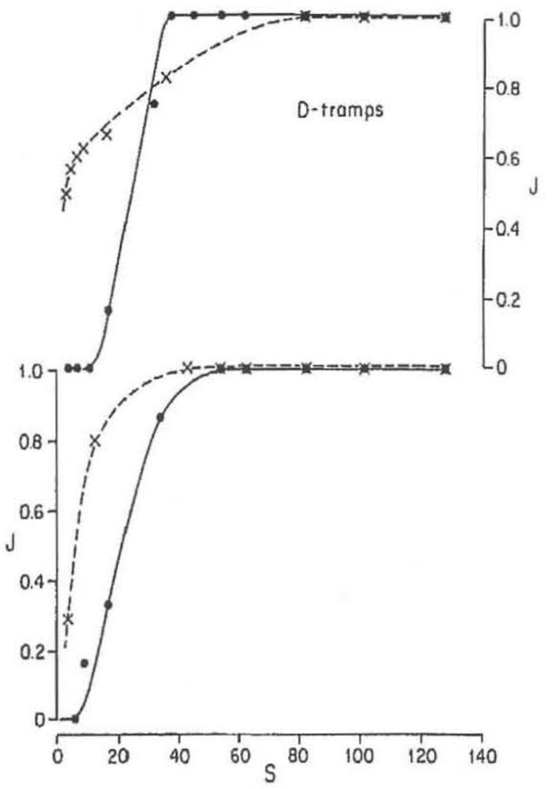


Figure 13 Incidence functions for various D-tramps in the Bismarcks. Above, points ● and line —, the hawk *Haliastur indus*. Points X and line – – –, the kingfisher *Halcyon saurophaga*. Below, points ● and line —, the starling *Aplonis metallica*. Points X and line – – –, the incubator-bird *Megapodius freycinet*.

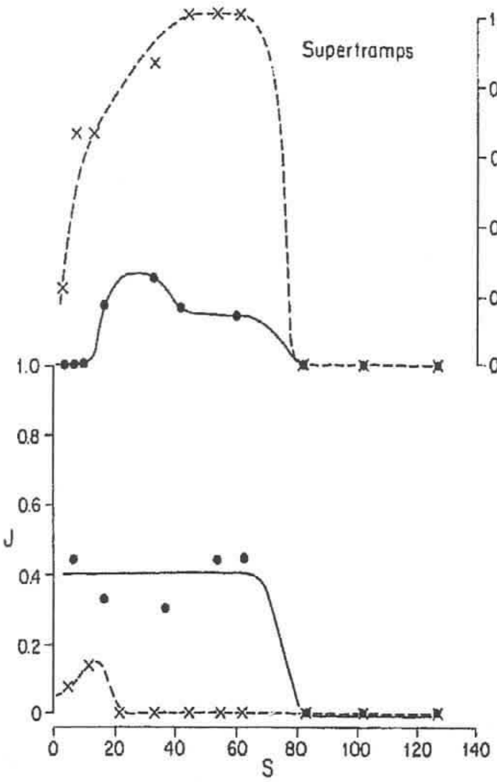


Figure 14 Incidence functions for various supertramps in the Bismarcks. Above, points X and line – – –, the pigeon *Ducula pistrinaria*. Points ● and line —, the white-eye *Zosterops griseotincta*. Below, points ● and line —, the whistler *Pachycephala melanura dahli*. Points X and line – – –, the starling *Aplonis feadensis*.

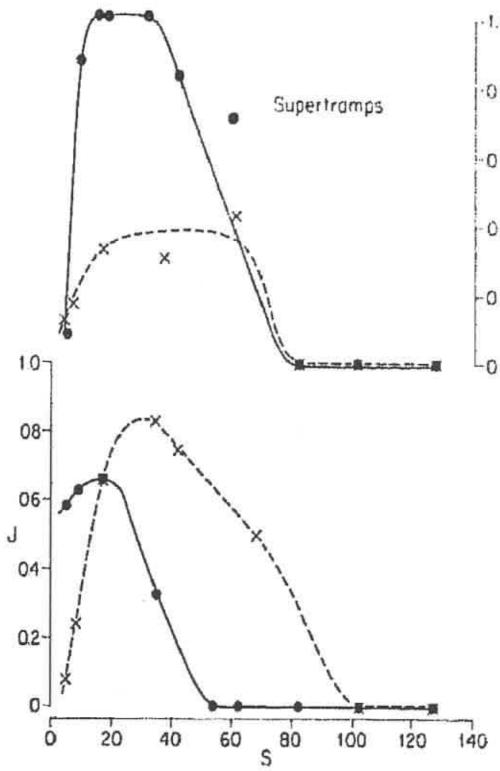


Figure 15 Incidence functions for various supertramps in the Bismarcks. Above, points ● and line —, the flycatcher *Monarcha cinerascens*. Points X and line – – –, the honeyeater *Myzomela sclateri*. Below, points ● and line —, the honeyeater *Myzomela pammelaenu*. Points X and line – – –, the pigeon *Ptilinopus solomonensis*.

Figures 4–15 are examples of incidence functions based on 50 well-surveyed islands of the Bismarck Archipelago, the group of islands extending from New Britain to Manus and lying between New Guinea and the Solomon Islands (Figure 1). A detailed analysis of the Bismarck avifauna, including species lists for each island, is given by Mayr and Diamond (1975), and speciation in the Bismarcks and Solomons has been discussed by Mayr (1969). Within the Bismarck Archipelago most of th[illegible] counted for by variation in area A, but some variation in S is also due to variation in isolation or to variation in elevation. Thus, the abscissa scale of Figures 4–15 is approximately but not perfectly equivalent to an A^z scale, where z (or x in the terminology of May, Chapter 4, eq. 5.1) is the exponent of area in the species/area relation. In general, if one constructs incidence functions $J_i(S)$ for all i species of an archipelago, the relation

$$\sum_i J_i(S') = S' \qquad (3)$$

holds for any arbitrary value $S = S'$.

The most obvious and immediate conclusion of Figures 4–15 is that the incidence function $J(S)$ may assume very different forms for different species. That is, the fauna of any island of any size, large or small, is a highly nonrandom selection of the archipelago's species pool and is systematically biased by island size (and, to some extent, by island elevation, isolation, and historical effects such as land bridges). Figures 4-6 assemble, for comparison, examples of the main types of incidence functions, and Figures 7–15 give further examples of each type of function.

Species distributions define a spectrum of incidence functions, which may be divided into six arbitrary categories. Table 1 summarizes, for each category, the number of species in the category, the range of number of islands inhabited by each species, the habitat preferences of each species, and the level of endemism of each species (i.e., whether the Bismarck population represents a full species, semispecies, or subspecies endemic to the Bismarck Archipelago, or belongs to the same subspecies as populations outside the Bismarcks). Table 1 also summarizes upper and lower values of critical species number, or so-called S_{crit} values, for each category. The meaning of S_{crit} values is that, for many species (see Figures 4, 5, 6 below, 7-9, 11 above, and 12), the incidence $J(S)$ decreases with decreasing S and goes to zero at some value of S that we may term the lower critical value or S_{crit}. For most species $J(S)$ approaches 1.0 or at least some nonzero value with increasing S, the highest S on any single island of the archipelago being 127. However, some species (Figures 6 below, 14, 15) also have an upper S_{crit} value, such that $J(S) = 0$ for higher S.

The six categories may be briefly described in words as follows:

One category (Figures 6 below, 14, 15), which we shall term "supertramps," consists of species characterized (by definition) by an upper S_{crit} and entirely absent as residents on species-rich islands (see Table 6 for a complete list). Several of the supertramp species (e.g., starling *Aplonis feadensis*) have an upper S_{crit} of only 16, i.e., are confined to islands with 16 or fewer species. It will be shown that supertramps represent the extreme of *r*-selection, in MacArthur-Wilson terminology. Only two supertramp species (cf. the pigeon *Macropygia mackinlayi,* Figure 6) have a lower S_{crit}; all other supertramps have a nonzero incidence on even the smallest or most species-poor islets. The geographical limits of most supertramp species extend beyond the Bismarcks, but most have evolved endemic subspecies in the Bismarcks.

The opposite extreme consists of species confined to the most species-rich islands (Figures 4 above, 7). It will be shown that some, but not all, of these high-S specialists represent the extreme of what is considered to be K-selection in MacArthur-Wilson terminology. We shall arbitrarily delimit a category of high-S specialists as consisting of species confined to the four most species-rich Bismarck islands ($S = 81$–127) plus not more than one island with 43–80 species. The great majority of the endemic species (8 out of 10) and semispecies (21 out of 28) of the Bismarcks belong to this high-S category. However, it is not true that, conversely, a great majority of high-S species are endemics: only a slight majority (56%) are

Table 1. Distributional categories in the Bismarck Archipelago

Category	No. species in category	No. islands inhabited per species	Endemism level				Lower S_{crit}			Upper S_{crit}		
			None	Subspecies	Semispecies	Species	<10	15–31	>32	≤ 16	45–83	None
High-*S*	52	1–5	9	14	21	8	0	0	52	0	0	52
A-tramp	26	3–9	8	14	3	1	1	1	24	0	0	26
B-tramp	17	10–14	4	12	1	0	3	5	9	0	0	17
C-tramp	19	15–19	8	10	1	0	6	9	4	0	0	19
D-tramp	14	20–35	9	5	0	0	11	3	0	0	0	14
Supertramp	13	2–33	2	8	2	1	10	2	1	4	9	0

For each of the six distributional categories listed in column 1 and defined in the text, column 2 gives the number of species in the category. Column 3 gives the range of number of islands inhabited by the species in the category (e.g., the entry 1–5 for high-*S* species means that the most widely distributed high-*S* species occurs on five islands, whereas some high-*S* species occur on only one island). Columns 4–7 give the number of species in the category endemic to the Bismarcks at the indicated level (none = not differentiated even subspecifically, subspecies = endemic subspecies, semispecies = endemic semispecies or allospecies of a superspecies, species = endemic full species). Columns 8–10 and 11–13 give the number of species in the category with the indicated lower and upper S_{crit}, respectively (e.g., 4 C-tramps are confined to islands with 32 or more species, 9 C-tramps reach at least one island with 31 or fewer species but no island with fewer than 15 species, 6 C-tramps reach islands with 10 or fewer species, and all 19 C-tramps lack an upper S_{crit} and have nonzero incidence on even the largest islands). It happens that no species has a lower S_{crit} value of 10–14 or an upper S_{crit} value of 17–44. Note that as one proceeds from supertramps to high-*S* species, the species tend to become endemic at higher levels (supertramps fall somewhat out of line as regards endemism) and to be confined to increasingly species-rich islands. The analyses in this table, Tables 2–6, and the text are based on all Bismarck bird species except for approximately a dozen that are difficult to assign to distributional category. Most of the omitted species are ones that have a wide range outside the Bismarcks and are confined in the Bismarcks to one or two peripheral, medium-sized islands at the edge of the species' geographical range.

endemic to the Bismarcks at the semispecies or species level, and a large minority (44%) have evolved only endemic subspecies or have not differentiated at all. This suggests that high-S species are a heterogeneous group, as will be confirmed by other evidence.

The remaining species are "tramps" that occur on the most species-rich islands but also on varying numbers of the poorer (smaller, or more remote) islands. We shall divide tramps into four arbitrary categories according to the total number of Bismarck islands inhabited: A-tramps on 3–9 islands, B-tramps on 10–14 islands, C-tramps on 15–19 islands, and D-tramps on 20–35 islands. When defined in this way, A-tramps prove to be almost exclusively confined to islands with more than 32 species; half of the C-tramps reach some islands with 15–29 species (as well as richer islands); and most of the D-tramps reach some islands with only 4–10 species (as well as richer islands). The level of endemism decreases progressively as one passes from high-S species to A-, B-, C-, and finally D-tramps, and then increases slightly again with supertramps. There are no endemic species among the B-, C-, and D-tramps, and most D-tramps have not even differentiated subspecifically.

Is the distribution of a given species determined by island area alone, so that we should properly speak of large-island and small-island species rather than of high-S species and supertramps? Or, do individual species distributions depend on distance as well as on area? Or, is S itself the relevant variable, some species being able to fit only into diverse communities and others only into poor communities? Expressed in another way, is S the best choice of abscissa for the incidence functions, or would area be a better choice? Detailed answers to these questions cannot yet be given. The answers are certain to be complex and must vary with the particular species considered. However, several preliminary conclusions can be drawn. First, for some species with lower S_{crit} values that are low but nonzero (e.g., C- and D-tramps reaching islands with 10 or 15 species but not reaching poorer islands), the S_{crit} value seems to be determined by minimum territory or minimum area requirements. In this case area is the significant variable. Second, we shall see that some species are excluded by certain combinations of other species; and that large land-bridge islands slowly relaxing towards equilibrium, and with S values presently greatly in excess of equilibrium values for their area, have compositions of some species guilds appropriate to their S and inappropriate to their area. In both of these cases S rather than area may be the more directly relevant variable. Third, some insight can be gained by making use of the fact that the Bismarck island that is third in area (Manus) is only twelfth in S, because it lies some 200 miles from the four other large islands (New Britain, New Ireland, New Hanover, and Umboi). No species is confined to and shared by the three largest Bismarck islands (New Britain, New Ireland, Manus), but 31 species have distributions confined to and shared by islands some of which are much smaller than Manus but all of which are more species-rich than Manus. Thus, the distribution of these species does not depend on large area alone; either they are stopped by the distance to Manus, or else they require high-S communities, whatever the factors that produced the high S. Finally, the relative proportions of high-S species, A-, B-, C-, and D-tramps, and supertramps on Manus are *fairly* similar to the proportions on six islands with similar S values but progressively decreasing area (down to 1% of the area of Manus) and increasing proximity to the large Bismarck source islands. More detailed examination indicates that if one maintains S constant by increasing island area with increasing distance from the largest and richest island (New Britain), the proportion of high-S species and A-tramps is higher on large distant islands (like Manus) and on small close islands than on medium-size islands of intermediate distance. This suggests again that the categories of high-S species and A-tramps are heterogeneous and consist partly of species limited by dispersal, partly of species limited by other factors.

Relation Between Incidence Functions and Habitat Requirements

To what extent are restricted species distributions due to restricted availability of required habitat? Habitat diversity is likely to correlate with island size (hence with bird species number). Three habitats (lowland forest, lowland aerial, and seacoast) exist on every Bismarck island, but five habitats (fresh-water lakes or streams, mangrove, mountains, open country or grassland, and marshes or swamps) may be entirely absent from small islands and present only in limited amounts on large islands. Species confined to these five scarce habitats must have zero incidence on small islands devoid of the habitat, and low incidence on islands with small areas of the habitat. For example, 13 species are confined to high elevations in the Bismarcks. Only five Bismarck islands exceed 3500 feet in elevation; one of these is a small island (18 square miles) and another was recently defaunated by a volcanic explosion. Naturally, the 13 montane species are restricted to these five islands, and 12 of the species are restricted to the three larger or nondefaunated mountainous islands. Similar examples can be cited for water birds, grassland birds, marsh birds, and mangrove birds.

Table 2 summarizes the habitat requirements of the species in each of the six incidence categories. All of the supertramps, and almost all of the D- and C-tramps, can live in one of the three ubiquitous habitats that exist on any island. However, half of the high-S species, and one-third of the A- and B-tramps, are confined to the five scarce habitats that occur only on certain islands. This indicates that up to 43% of the species with restricted island distributions (high-S species, A- and B-tramps) could possibly be restricted by habitat availability, whereas 57% are not.

Table 3 summarizes the endemism level of species in each incidence category according to habitat requirement. For this purpose we assemble habitats into three groups: ubiquitous (lowland forest, low-

Table 2. Species habitat preferences, by distributional category

Habitats	Species					
	High-S	A-tramp	B-tramp	C-tramp	D-tramp	Supertramp
Ubiquitous habitats						
Lowland forest	25	16	12	13	8	13
Sea coast	0	0	0	2	3	0
Lowland aerial	0	1	0	3	1	0
Subtotal	25	17	12	18	12	13
Scarce habitats						
Fresh water	5	1	1	0	0	0
Mangrove	2	0	0	0	0	0
Montane	12	1	0	0	0	0
Open country	5	6	4	1	2	0
Marsh, swamp	3	1	0	0	0	0
Subtotal	27	9	5	1	2	0

For each Bismarck distributional category, the table lists how many species in each category live in each of the three "ubiquitous" habitats that occur on every island, and how many species are confined to each of the five "scarce" habitats that occur only on certain larger islands. A species is assigned to the category "lowland forest" if it lives in lowland forest on some islands; some tramps that live in lowland forest on species-poor islands are competitively excluded from forest and restricted to forest edge on species-rich islands. Note that almost all lowland aerial and sea-coast species are widespread (C- or D-tramps), that most species of scarce habitats have restricted distributions (high-S species, A- or B-tramps), that almost all montane birds have very restricted distributions (high-S species), and that almost all widespread species (most C- and D-tramps, all supertramps) are in ubiquitous habitats.

land aerial, sea-coast); montane; and scarce lowland (fresh-water, mangrove, grassland, and marsh). The scarce habitats have been separated into montane and lowland, because these two groups behave very differently as regards endemism. Table 3 and the detailed distributions on which it is based yield the following conclusions:

1. Endemic species are entirely (10 out of 10), and endemic semispecies are largely (24 out of 28), confined to lowland forest or mountains. Only 5 of these 38 endemics occur on more than 9 Bismarck islands, the remaining 33 endemics being high-S species or A-tramps.

2. Conversely, 12 out of 13 montane species have differentiated at least at the subspecies level, and 7 out of 13 have differentiated further. All montane species are high-S species except for one A-tramp.

3. Most of the high-S species and A-tramps that are confined to scarce lowland habitats (19 out of 23) have failed to differentiate beyond the subspecies level. In contrast, of the high-S species and A-tramps in lowland forest, half (22 out of 42) have differentiated beyond the subspecies level.

4. Not a single one of the 9 B-, C-, and D-tramps confined to scarce lowland habitats has differentiated beyond the subspecies level. In addition, only a few (3 out of 13) of the supertramps, and almost none (just 2 out of 41) of the B-, C-, or D-tramps, in widespread lowland habitats have passed the subspecies level.

In most cases, low endemism can probably be interpreted to mean high dispersal rates between Bismarck islands, and be-

Table 3. Levels of endemism, by habitat preference and distributional category

Category	Endemism level			
	None	Subspecies	Semispecies	Species
High-*S*	1/1/7	5/4/5	12/6/3	7/1/0
A-tramp	4/0/4	10/1/3	2/0/1	1/0/0
B-tramp	2/0/2	9/0/3	1/0/0	0/0/0
C-tramp	8/0/0	9/0/1	1/0/0	0/0/0
D-tramp	6/0/3	5/0/0	0/0/0	0/0/0
Supertramp	2/0/0	8/0/0	2/0/0	1/0/0

In each entry, the first, second, and third numbers give the number of species, respectively, in ubiquitous habitats (lowland forest, sea-coast, lowland aerial), confined to mountains, or confined to scarce habitats other than montane habitats (fresh water, mangrove, open country, marshes and swamps). For each of these three habitat categories, the table gives how many Bismarck species in each distributional category are endemic at the indicated level. See text for discussion.

tween the Bismarcks and neighboring archipelagoes. This criterion would suggest the following conclusions:

1. Most species confined to scarce lowland habitats have high dispersal rates, whatever the form of their incidence function. It is adaptive for species in these habitats to have high dispersal rates so as to make up for the high extinction rates of their populations, associated with the small areas of the habitat patches and instability of the patches.
2. All lowland aerial and sea-coast species in the Bismarcks without exception have high dispersal rates. (This is not so strictly true, however, for the New Guinea region, where there are several swifts that have failed to colonize a single island.)
3. In lowland forest, almost all of the widespread species, and half of the high-*S* species and A-tramps, have high dispersal rates. The remaining half of the high-*S* species and A-tramps have low dispersal rates.
4. Almost all montane species have low dispersal rates.

Although conclusions about dispersal based on degree of endemism are not unassailable, these conclusions are confirmed by the direct observations of dispersal to be discussed in the section "Relation between incidence functions and dispersal." These relations between habitat preference, degree of endemism, and geographical range for Bismarck birds share some similarities with the corresponding relations for Melanesian ants, as formulated by Wilson (1961) and described as the "taxon cycle." Colonization of the Bismarcks by birds has originated almost exclusively from New Guinea. Evidently most of the colonists disperse initially into lowland forest and nonforest habitats, and many of them initially retain the high interisland dispersal rates that enabled them to reach the Bismarcks in the first place. With time, many of the colonists lose their dispersal ability, become extinct on most small or species-poor islands, adapt to forest or shift entirely into forest, and sometimes shift into montane forest. One of the differences between birds and ants on New Guinea is that most colonizing ants occupy lowland nonforest habitats and enter forest only on reaching a species-poor island, whereas many colonizing birds already occupy lowland forest. These relations are discussed in detail by Mayr and Diamond (1975).

For the present, we note that high-S species and A-tramps are actually a mixture of two types of species: birds whose absence from small islands is due to specialized habitat requirements; and birds that live in ubiquitous habitats and whose absence from small islands must be interpreted in other ways.

Relation between Incidence Functions and Island Area

Since the sum of all incidence functions equals total species number (eq. 3), and since area contributes most of the variation in species number, the interpretations of incidence functions and of the species/area curve must be closely related. There is an extensive literature on the interpretation of the species/area relation (Preston, 1962; MacArthur and Wilson, 1967; May, Chapter 4, Section 5). Despite this literature it is still neither simple nor generally agreed how to answer the simple question, "Why do smaller islands have fewer species?" Let us examine the ways in which area affects species distributions in the light of examples from the New Guinea region. We begin with trivial effects and proceed to more interesting ones.

Absence of suitable habitat.

Small islands may entirely lack certain habitats and hence species restricted to these habitats. For instance, ponds and permanent streams in the Bismarcks require a large watershed, and natural grassland requires mountains high enough to create a rainshadow; hence these habitats are lacking on most Bismarck islands smaller than 15 square miles. The lower S_{crit} values of species of these habitats, such as the duck *Anas superciliosa,* the montane river flycatcher *Monachella muelleriana,* the montane honeyeater *Melidectes whitemanensis,* the grass warbler *Cisticola exilis,* and the grass nightjar *Caprimulgus macrurus,* are due to this reason.

Island size less than minimum territory requirement.

Depending on the territory size of a single pair, there will be some minimum island size below which a single pair of even a highly vagile species cannot exist, even if the entire surface of the island is covered by suitable habitat. For example, the eagle *Haliaeetus leucogaster* forages over a territory of about 5–15 square miles. On islands smaller than this range, a resident pair of this eagle cannot maintain itself. The lower S_{crit} values of some other rapidly dispersing C- and D-tramps that maintain pair territories, such as the hawks *Haliastur indus* and *Accipiter novaehollandiae,* the herons *Nycticorax caledonicus* and *Ixobrychus flavicollis,* and the dollarbird *Eurystomus orientalis,* may also correspond to an island area comparable to the territory of one pair.

Seasonal or patchy food supply.

In the great majority of temperate-zone bird species, a single pair of birds defends an exclusive breeding territory against conspecific birds. This is possible because all resources that the pair needs are available within an area small enough to be feasibly defended. For many tropical species, however, the required resources are patchily distributed both in time and in space. Karr (1971) has shown that many such species in Panama lowland forest have large territories held jointly by a flock of individuals, or else large, extensively overlapping territories each held by a pair, rather than a smaller, exclusive and self-sufficient territory. All the individuals sharing these large territories may depend upon food in one part of the territory in one month, in another part in another month.

To an observer in the southwest Pacific, it becomes obvious that patchy and seasonal availability of food supply is important especially for fruit-eaters, seed-eaters, and species dependent on flowering trees. For example, a guild of pigeon species specializes on tall trees bearing soft fruits, whereas a guild of lorikeets and honeyeaters specializes on nectar and insects obtained from flowering trees. When a particular tree transiently comes into fruit or flower, dozens of birds congregate to feed. Yet suitable feeding trees may be spaced a mile or more apart, even in an area where fruiting or flowering is occurring (Terborgh and Diamond, 1970). Correlated with the cycle of wet and dry seasons, the occurrence of fruiting and flowering shifts from locality to locality throughout the year, and the associated bird guilds undertake local seasonal movements (Diamond, 1972a). These seasonal movements have been documented not only for fruit-eaters (*Ptilinopus* and *Ducula* pigeons, *Aplonis* starlings, the cuckoo *Eudynamis scolopacea*, etc.) and flower-feeders (*Myzomela* honeyeaters, parrots of numerous genera), but also for seed-eaters such as *Lonchura* finches, and some insectivores such as *Collocalia* swiftlets, the tree swift *Hemiprocne mystacea*, the swallow *Hirundo tahitica*, and the flycatcher *Rhipidura leucophrys*.

The result of these seasonal shifts in food supply is that an island that seems to an ornithologist large and covered with fruits and flowers still may not be able to support the expected bird guilds, unless a food supply is available within the island's confines for all twelve months of the year. Availability of a year-round food supply may require sufficiently varied topography to cause local intra-island variation in fruiting or flowering season (due to intra-island variation in slope, exposure, rainfall, and altitude). Thus, either an island does provide a year-round food supply and supports an entire flock of a species, or else it supports no individuals of the species at all. Even on an island as large as Sakar (17 square miles), the small resident flock of the flower-feeding parrots *Vini placentis, Trichoglossus haematodus*, and *Lorius hypoinochrous* could be seen flying back and forth among a few flowering trees at opposite ends of the island. The requirement that an island be large enough to provide a year-round food supply is probably the reason for the lower S_{crit} values in some incidence functions of species dependent on shifting or patchy food, such as the D-tramp parrot *Trichoglossus haematodus* or the C-tramp parrot *Vini placentis*. The incidence function of the former parrot is very steep, falling from $J = 1.0$ at $S = 15$ to $J = 0$ at $S = 9$.

In the cases discussed above, resource seasonality or patchiness is due to seasonality or patchiness in resource production itself. For some other tropical species, resource *availability* may be patchy despite widespread resource *production*, because most of the resources are preferentially consumed by a diverse constellation of competitors. Suppose that a guild consists of many species with broadly overlapping resource-utilization functions, but that each species has a competitive advantage in a different region of the resource or habitat spectrum. Then a given species will find resources available to it only at those scattered points in time or space where it has a competitive advantage or where some of its competitors are absent (see Figure 44). This may be the reason why, among New Guinea birds as among the Panama birds Karr studied, individuals of some insectivorous species as well as frugivorous species associate in flocks or have overlapping territories or are patchily distributed.

Thus, seasonal or patchy food supplies may directly reflect patterns of resource production, but may also be created by the activities of a guild of overlapping consumers. In either case, a species can persist on an island only if the area is sufficient to provide a year-round food supply.

Population fluctuations.

We have discussed the three preceding effects of area as all-or-nothing effects—as if an island either were big enough to hold a given species, or else not big enough, with no intermediate states. Had this all-or-nothing interpretation been true, some incidence functions might have been step functions, which is never the case. In fact, of course, an important ingredient of the MacArthur-Wilson equilibrium theory, developed further by Leigh (Chapter 2), is that a population of any given size runs a finite risk of extinction due to population fluctuations, and that this risk increases with decreasing population size. Let us consider four examples illustrating this risk:

(a) Table 4 summarizes bird censuses on five small islets, ranging in area from 0.8 to 12.8 acres, and supporting from 3 to 7 species. Of the 23 populations on these islands, 12 consisted only of a single individual, 5 of two individuals each, 3 of three individuals each, 2 of five individuals each, and 1 of 18 individuals. Thus, most of these populations were so small that the death of a single individual would either eliminate the population or else remove its potential for reproduction. These populations must go extinct so often that only the most rapidly recolonizing species can exist on such small islets. In practice, 20 of the 23 populations were either supertramps or D-tramps. Four of the 23 populations (one supertramp and three D-tramps) belonged to species that certainly or possibly move from islet to islet in the course of their normal foraging, but the other 19 belonged to territorial species whose individuals probably spend their whole adult lives on the islet on which they settle. It

Table 4. Bird censuses on small islets

Islet	Area (acres)	Number of species	Population size (number of individuals)				
			18	5	3	2	1
Midi	6.3	7	—	—	—	3	4
Hein	12.8	5	—	—	2	1	2
Matenai	1.6	4	—	1	—	1	2
Araltamu	0.8	4	—	1	—	—	3
Little Pig	2.9	3	1	—	1	—	1

For each coral islet column 2 gives the area; column 3, the number of resident Bismarck species found on the island; and columns 4, 5, 6, 7, and 8, the number of species whose island population consisted of 18, 5, 3, 2, and 1 individuals, respectively. The conclusion is that populations on small islets consist of few individuals and must be very unstable.

is not the case that these were probably vagrant individuals that were just flying by and had alighted; instead, these were the characteristic resident species of small islets.

(b) Crown, an island of 5 square miles, supports 30 species. Of these, two were represented by a single individual, one by a pair, two by three individuals, four by about five individuals, two by about five pairs, and one by about ten pairs. Sakar, an island of 15 square miles, supports 36 species. Of these, two were represented by a single individual, two by a pair, one by three individuals, seven by about five individuals, and four by about five pairs. For many of the 28 marginal populations on these two islands, there were obvious reasons why the population was so small: four were species that could utilize the whole island area but required large pair territories (e.g., the eagle *Haliaeetus leucogaster,* the forest heron *Nycticorax caledonicus*); eight were species that could utilize only small fractions of the island area as habitat (e.g., the coastal heron *Egretta sacra,* the grassland bee-eater *Merops philippinus*); and five were flower-feeding parrots that maintain a large flock territory. Two or three of the species on each island wander routinely among islands as adults, but the remaining species are ones that probably spend their adult lives on one island. Thus, even on islands as large as 5 or 15 square miles, about 40% of the populations are small enough to face a high risk of extinction. This point is worth mentioning in view of the erroneous assumption sometimes made that island populations are generally abundant and therefore immune to risk of extinction arising from population fluctuations.

(c) When rising sea-level severed late-Pleistocene land bridges, populations of New Guinea lowland species stranded on the resulting land-bridge islands began selectively to go extinct (Diamond, 1972b). Today there are 32 species that are widespread in the New Guinea lowlands but absent from every single land-bridge island, including islands as large as 3000 square miles. For most of these species the land-bridge islands must formerly have supported populations, which must therefore have disappeared after the land bridge was severed. In most cases it is clear that these initial populations must have been very small and extinction-prone. Three of the species live in forest but require very large territories (e.g., the New Guinea Harpy Eagle *Harpyopsis novaeguineae*); 13 species live in forest and do not have very large territories but live at low densities (e.g., the kingfisher *Clytoceyx rex*, the bird of paradise *Drepanornis bruijnii*); 13 species are nonforest birds with specialized habitat requirements (e.g., the swamp rail *Megacrex inepta*, the grass warbler *Malurus alboscapulatus*); and nine species, including some of the above ones, depend on seasonal and patchy supplies of fruit, flowers, and seeds. Only two widespread and common forest species disappeared from all land-bridge islands without obvious reason. Wilson and Willis (Chapter 18, Table 1) document similar selective extinctions of bird populations on Barro Colorado Island, and Brown (1971) did so for mammal populations on mountaintops of the Great Basin.

(d) Equilibrium turnover studies have been carried out on three Bismarck or New Guinea islands: Karkar, Vuatom, and Long. Of the 13 populations that disappeared, nine were small because of being confined to specialized habitats or because of a large territory requirement. The remaining four populations were fruit-eaters or flower-feeders dependent on a patchy, seasonal food supply. Turnover studies on the California Channel Islands have similarly shown that populations that for one reason or another (scarce habitat, large territory, recency of colonization, small island, presence of a close competitor) consist of few individuals are the ones most likely to go extinct (Diamond, 1969, 1971; Jones and Diamond, 1975).

As a final general point about area-dependent extinction rates due to fluctuations in small populations, the significance of rare events and long-term fluctuations should not be underestimated. For normally large populations, the risk of extinction due to stochastic variation in births and deaths will be negligible. Much more significant is the risk of extinction when the population has crashed temporarily to a low level following a rare event (i.e., the problem of resilience as opposed to steadiness, in the sense of Leigh, Chapter 2), such as the drought that occurred in the Madang area in 1972; forest fires, such as the one that swept the Madang lowlands 50 years ago; temporary local superabundance of other bird species, such as is associated with the seeding of some bamboo species once or twice a century; invasions of other species, such as the invasion of New Zealand around 1856 by *Zosterops lateralis* (now one of the most abundant New Zealand birds); cyclones, such as the one that blew down much of the forest on Ngela and Santa Ysabel islands in 1972; volcanic explosions and the resulting ash fall-out, such as occur often along the south edge of the Bismarck Sea; and tidal waves, such as one that inundated the islands of Dampier

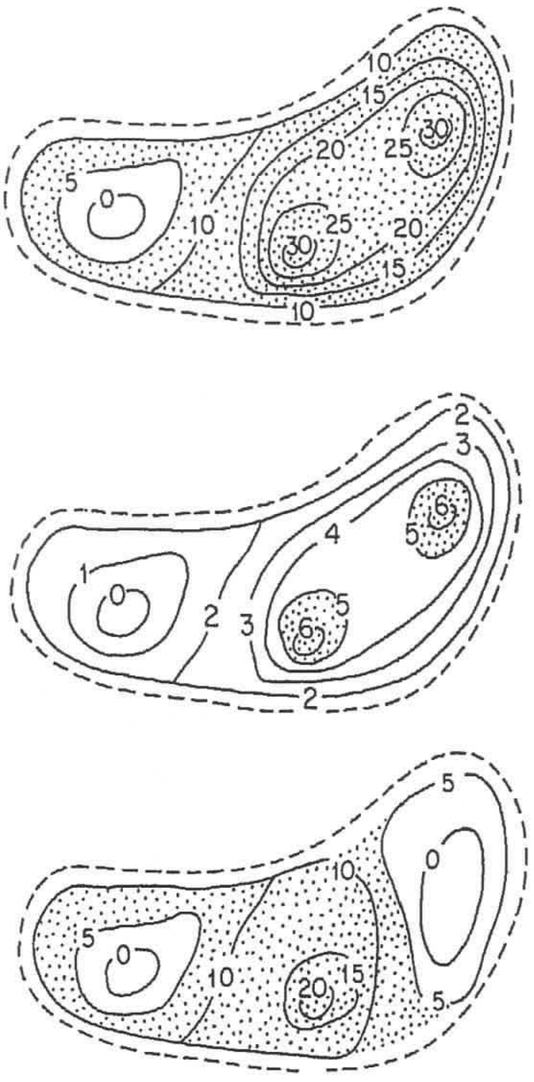


Figure 16 Hypothetical example of the importance of "hot spots." The example refers to a forest bird species on a forested island (coast line indicated by dashed outline), on which the rate of production of resources utilizable by the species (R) varies locally with exposure, slope, and soil type. Contours connect points with equal values of R, in arbitrary units. The species can survive only in areas where $R > 5$, distinguished by stippling. Above: situation in the absence of a competitor and during a productive year. The species occupies most of the island except the unproductive "cold spot" near the west end. An especially productive area in the center and another at the east end ($R > 25$) function as "hot spots," where steady-state population density is highest, and where the species could increase most rapidly if it were initially colonizing the island or reexpanding after a population crash. Middle: same, except that R is uniformly reduced by 80% over the whole island, either because of an unproductive year, or because of an abundant competitor that utilizes the given resources in the same proportion. The species now can survive only on the two hot spots. Below: as in top sketch except that the island has now been invaded by a competitor with an overlapping but different resource utilization, such that the competitor cannot survive at the west end but becomes increasingly common towards the east end. The original species still occupies most of the island, but only one of the two spots is left. This illustrates that hot spots depend not only on local microhabitat variation in relation to a species' requirements, but also on microhabitat variation in relation to the requirements of competing species.

Strait in 1888. These events may be rare on the time-scale of an ornithologist's scientific career, but common on the time-scale of population lifetimes for species with low dispersal rates. If the recolonization frequency is comparable to or lower than the frequency of disaster-induced population crashes, the incidence of a species on otherwise suitable islands must be significantly less than 1.

"Hot spots."

Especially on large islands one must take account of the fact that even within suitable habitat the area inhabited by an established species, or else the area potentially available to an invading species, is not all equally suitable. The rate of production of those resources that can be utilized by a given species varies locally, both as a function of the physical environment and as a function of the distributions of competing species in the same guild. If one connects points with equal resource levels by contours analogous to isotherms, areas of especially high utilizable resource production stand out as "hot spots." The presence of competing species, or a year of low production, may submerge resource levels over most of an island below minimum support levels, leaving the hot spots as islands of supraminimal resource production and hence as distributional islands (Figure 16). In general, the number or total extent of hot spots will increase with island area. For many species this may be the principal reason why, on large islands, rates of successful immigration continue to increase with increasing island area. It may also, in conjunction with population fluctuations, be for many species the main reason why extinction rates continue to decrease with increasing island area on large islands.

Consider a newly arrived species on an island sufficiently large that, if the species could equilibrate over the island, its population would be large enough to be virtually extinction-proof. Whether the species actually succeeds in reaching this saturating population level *K* depends on whether it escapes extinction in the initial phase of very small numbers. In this phase, the immigrant's chance of success depends upon the presence of hot spots where it can quickly start generating a population surplus. An immigrant that can adequately search an island would be expected to select the hot spots for its first settlement. In fact, even for organisms of high dispersal ability such as birds, recent immigrant populations on a large island are often very local. For example, in 1933 the sole fruit pigeon of genus *Ptilinopus* on Long Island was *P. solomonensis*. At some time between 1933 and 1972, the related *P. insolitus* invaded. In 1972, *P. insolitus* was well established at 500–1500 feet on the northeast ridge of Mount Reumur but was encountered nowhere else on Long. Since *P. insolitus* and *P. solomonensis* coexist on numerous islands smaller than Long, the chances of eventual success for an invasion by *P. insolitus* must be rated a priori as excellent. By comparison with other islands, *P. insolitus* may finally come to share all of Long from sea level to about 2000 feet with *P. solomonensis*. Thus, the northeast ridge of Mount Reumur may constitute a hot spot that permitted *P. insolitus* quickly to pass through the early critical phase.

Correspondingly, consider a species in risk of extinction on a large island. Hot spots are the most likely place for the species to make its last stand, or to be saved from extinction at the last moment. If a year of low production drastically reduces the population and the species contracts back to the hot spots, it may then quickly escape danger by producing population surpluses from the hot spots in better years and reexpanding over the island. If the species does finally go extinct, hot spots may have permitted it to escape the inevitable end for a long time. The fact that the larger land-bridge islands around New Guinea still have double their equilibrium species number, more than 10,000 years after the land bridges were severed, emphasizes for what long times many species can escape their inevitable doom on a large island. The distributions of numerous patchily distributed bird species on New Guinea itself are most plausibly interpreted in terms of gradual extinction and contraction onto hot spots. As illustrated in Figures 35–38 (see also Diamond, 1972a), many New

Guinea bird species that belong to distinct monotypic genera without close relatives (e.g., the bowerbird *Archboldia papuensis,* the cuckoo-shrike *Campochaera sloetii*), or else to large genera with many ecologically similar species (e.g., the honeyeater *Ptiloprora plumbea,* the berrypecker *Melanocharis arfakiana*), have fragmented, relict-like distributions with respect to the available habitat. Many of these species are probably slowly going extinct, either because they are the last survivors of unsuccessful evolutionary lines (monotypic genera), or because they are being outcompeted by ecologically similar congeners. For example, the Umboi population of the fruit pigeon *Ptilinopus solomonensis,* which was widespread in 1913 but is now probably doomed to extinction as a result of successful simultaneous invasions by two relatives, has contracted back to a small area at the base of Mount Birik. The flycatcher *Microeca leucophaea,* which was formerly widespread in the Port Moresby savanna of southeast New Guinea, has contracted since 1945 down to two local populations. Both of these cases probably exemplify species that are making their last stands on hot spots. Such species represent an appreciable fraction of the total species number on large islands like New Guinea.

Relation between Incidence Functions and Dispersal

Absence of a species from an island could be due to interesting competitive interactions, but it could also simply mean that no individuals of the species ever immigrated. Or, there might have been immigrants, but in too small numbers and at too rare intervals to yield much probability of success. Thus, before we can examine incidence functions for evidence of community integration and resistance to invasion, we need to know something about the relative rates at which species disperse. In the section "Relation between incidence functions and habitat requirements" we drew tentative conclusions based on degree of endemism. In this section we shall consider five, more direct, lines of evidence about dispersal ability.

Note that if a bird species is known never to cross a 10-mile water gap, we should not assume that it is physiologically and mechanically incapable of a 10-mile flight but that, much more likely, the species has an insuperable psychological barrier to crossing water. This reluctance of some strong-flying bird species, especially tropical species, to cross water gaps is insufficiently appreciated. For example, of the 325 bird species of the New Guinea lowlands, only 4 are flightless, yet only 191 have crossed water gaps more than 5 miles wide, as shown by their having been recorded from one or more islands lacking a recent land bridge. Figure 17 illustrates the distribution of the flycatcher *Monarcha telescophthalmus,* which occurs on every large island that had a Pleistocene land bridge to New Guinea but on no island that lacked a land bridge. The list of species absent from oceanic islands includes some soaring hawks, swifts, and itinerant parrots that fly 100 miles a day over the New Guinea mainland in the course of their normal foraging, and that could reach

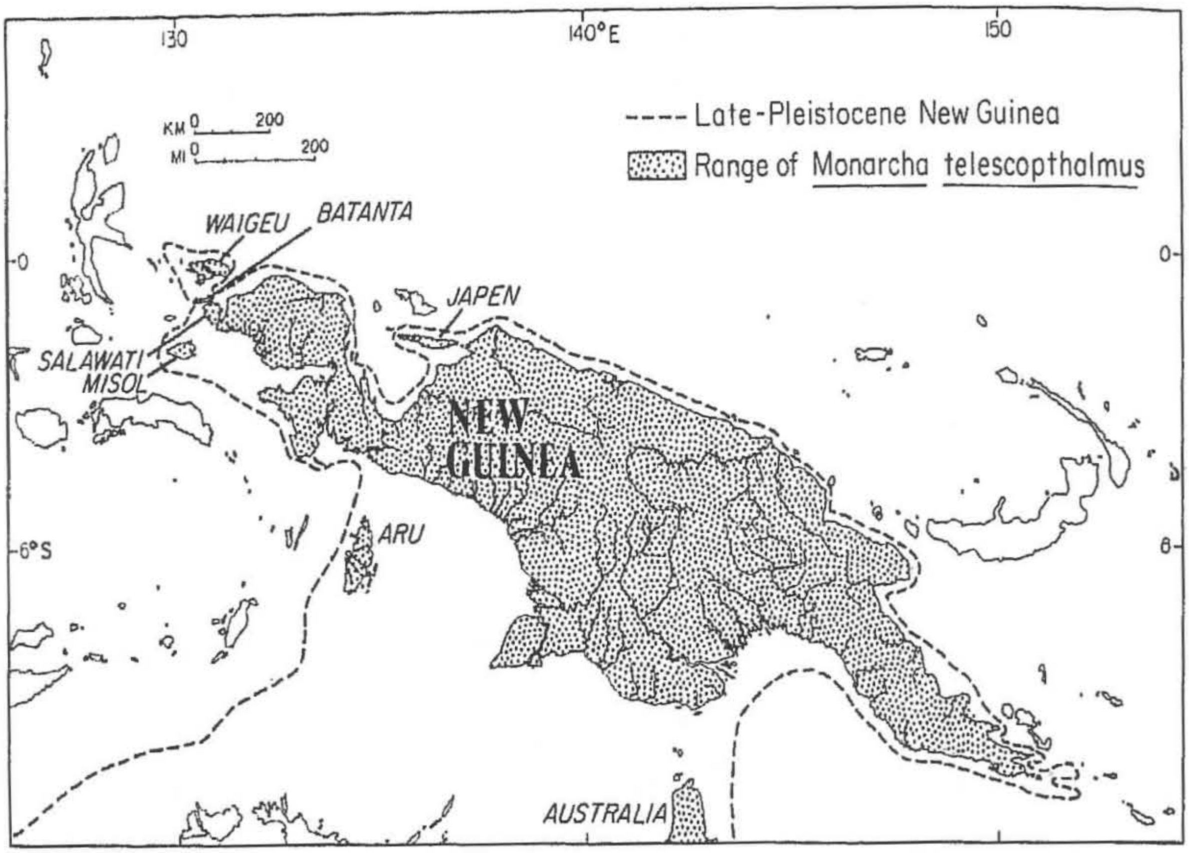


Figure 17 Distribution of the flycatcher *Monarcha telescophthalmus* (shaded islands). The dashed line is the contour of 200-m ocean depth, which is very close to the 100-m contour. The whole area within the dashed line formed a single land mass at times of lower sea level during the Pleistocene. Thus, present-day islands within this dashed line are "land-bridge islands." Note that this flycatcher now occurs on every large (>175 square miles) land-bridge island, named on the map, but on no oceanic island nor on any small land-bridge island, not even those within a few hundred yards of New Guinea. The cockatoo *Probosciger aterrimus* has the same distribution. Both species are capable of normal flight, and the cockatoo is a strong flier.

some large, close, readily visible offshore islands in a fraction of an hour, but never do. Similarly, hundreds of Asian bird species, including numerous whole families, have completely failed to cross Wallace's line separating the land-bridge islands of the Sunda Shelf from the deep-water islands of Indonesia. An even larger number of neotropical bird species, including the whole family Formicariidae with 221 species, have failed to reach any oceanic island off Central America or South America (MacArthur et al., 1972). Wilson and Willis (Chapter 18) note that many forest species have not crossed the water gap 500 meters wide separating Barro

Colorado Island from the Panama mainland. Even in the temperate zones, extensive records from the Channel Islands and Farallon Islands off California show that some strong overland fliers, such as the Common Crow *Corvus brachyrhynchos* and Red-shouldered Hawk *Buteo lineatus*, rarely or never cross water to reach California's offshore islands (Jones and Diamond, 1975). Thus, it would be a serious mistake to assume that all birds that can fly are potentially good colonists.

Let us now examine the direct evidence for dispersal abilities of species.

Recolonization of defaunated islands.

Two centuries ago, a volcanic explosion defaunated Long Island in the southwest Bismarcks, covering the island with nuées ardentes and ash deposits up to 100 feet thick or more. Long is 76 miles from the richest Bismarck island (New Britain) and 37 miles from the third-richest island (Umboi). By 1972, 54 bird species had recolonized Long, as detected by surveys in 1933 and 1972 (Diamond, 1974). These species are 10 of the 13 Bismarck supertramps, all 14 Bismarck D-tramps, 11 of the 19 C-tramps, 9 of the 17 B-tramps, 6 of the 26 A-tramps, 1 of the 52 high-S species, and 3 unclassified species. Of the A-tramps and high-S species, all but one (an endemic Bismarck subspecies) are species that have not differentiated even subspecifically in the Bismarcks, and all but one are species of scarce and unstable habitats (marshes, fresh water, grassland). Thus, all the colonists of Long are species that were suspected of dispersing rapidly on the basis of wide distribution and/or low endemism. Although species number in the lowlands of Long is already close to the equilibrium value predicted for Long's area, the number of Long's montane avifauna is far below equilibrium, in agreement with the postulated poor dispersal ability of montane birds. The sole obligate montane species that has recolonized Long is the sole montane A-tramp of the Bismarcks, the ubiquitous montane finch *Erythrura trichroa*, which opportunistically follows the seeding of bamboo.

Ritter Island in the southwest Bismarcks was defaunated by a volcanic explosion in 1888. In 1972, seven species were found on Ritter, four as residents and three as vagrants. These were three supertramps, one D-tramp, two C-tramps, and one nonendemic A-tramp (the Peregrine Falcon, which had also recolonized Long).

Seven small coral islets near Ritter were defaunated by the tidal wave caused by the Ritter explosion. In 1972 these islets supported a total of 45 populations: 17 supertramps, 24 D-tramps, 2 C-tramps, and 2 B-tramps.

Thus, the evidence from defaunated islands indicates that the highest dispersal rates are among supertramps and D-tramps, followed by C- and B-tramps and nonendemic A-tramps of scarce habitats. Dispersal of endemic forest A-tramps, high-S species, and montane species has been negligible.

Dispersal to Vuatom.

Vuatom Island is 4 miles offshore from New Britain, the largest and most species-rich Bismarck island. The area of Vuatom is 5 square miles, and its elevation is somewhat over 1000 feet. It supports forest, grassland, and permanent streams but lacks marshes and high mountains. The observations of Father Otto Meyer (1906, 1930), resident missionary on Vuatom for several decades, provide the best long-term record of vagrants in the Bismarck Archipelago.

In 1906, Father Meyer reported about 47 breeding species on Vuatom. By 1930, the populations of 5 of these breeding species had disappeared, 4 new breeding species had become established, and 24 other species that breed on New Britain and adjacent islands (plus 15 wintering species from Asia, Australia, and New Zealand) had appeared transiently but had not established breeding populations. Table 5 summarizes some facts about the successful and unsuccessful colonists.

By 1930 every Bismarck D-tramp, all but two each of the C-tramps and B-tramps, half of the A-tramps, and only 13% of the high-*S* species had been recorded from Vuatom. A similar sequence is obtained if one calculates the 1906–1930 arrivals (whether successful or unsuccessful) as a percentage of the available species pool not already resident on Vuatom in 1906. The low percentage of supertramp arrivals is initially surprising, but in fact the five species classified as supertramps that were not recorded have no populations within 150–250 miles of Vuatom.

Table 5. Colonization of Vuatom Island, 1906–1930

	Category					
	High-*S*	A-tramp	B-tramp	C-tramp	D-tramp	Supertramp
1. Total species for category	52	26	17	19	14	13
2. Resident species, 1906	1	11	11	11	8	5
3. Total colonists, 1906–1930	6	3	4	6	6	3
4. Successful colonists	0	0	1	0	2	1
5. Unsuccessful colonists	6	3	3	6	4	2
5a. On smaller island?	0	0	1	4	4	2
5b. On more species-poor island?	0	1	3	6	4	2
6. Available pool, 1906	51	15	6	8	6	8
7. 100 × total colonists/available pool	12	20	67	75	100	37
8. 100 × total recorded/total in category	13	54	88	89	100	62

For each of the six Bismarck distributional categories, row 1 gives the total number of species (from Table 1, column 2); row 2, the number breeding on Vuatom in 1906; row 3, the number of species that were not breeding on Vuatom in 1906 but at least one individual of which was observed on Vuatom any time between 1906 and 1930; row 4, the number of colonists listed in row 3 that had breeding populations on Vuatom in 1930; row 5, the number of colonists listed in row 3 that did not have breeding populations in 1930; row 5a, the number of unsuccessful colonists in row 5 that breed on at least one island smaller than Vuatom; row 5b, the number of unsuccessful colonists in row 5 that breed on at least one island with fewer species than Vuatom; row 6, the species pool available for colonization in 1906 (row 1 minus row 2); row 7, the percentage of this pool that did colonize between 1906 and 1930 (row 3 divided by row 6); and row 8, the percentage of all the species in the category that had been recorded from Vuatom by 1930 (row 2 plus 3, divided by row 1). The data are extracted from Meyer (1906, 1930).

Of the 28 arrivals (successful or unsuccessful), 14 have not differentiated racially in the Bismarcks, 8 have formed endemic subspecies, and only 6 (including 5 of the 6 high-*S* species) are endemic semispecies.

Of the 24 unsuccessful colonists, the preferred habitat type of all but one (a montane high-*S* species) was available on Vuatom. Table 5 summarizes for each of the unsuccessful colonists whether it has a resident population on any Bismarck island smaller than Vuatom, or on any Bismarck island with a smaller resident species total than Vuatom. All of the unsuccessful supertramps, D-, C-, and B-tramps occur on islands more species-poor than Vuatom, and most occur on smaller islands. Thus, there is nothing intrinsic in the size, species richness, or habitat spectrum of Vuatom that doomed these colonists to failure. Their failure is presumed to be due either to chance (as calculated by MacArthur and Wilson, 1967, Chapter 4, from the numbers and from the expectations of births and deaths of the colonists), or else to exclusion by competitors or constellations of competitors. A role of competition is indicated by the fact that 8 of these 15 plausible but unsuccessful colonists found congeners or close relatives already established on Vuatom. In contrast, of the 9 unsuccessful high-*S* species and A-tramps, none has a resident population on an island smaller than Vuatom, and only one on a more species-poor island. Thus, incidence functions would already have forewarned us that these colonists were doomed to failure. A role of competition in these cases as well is indicated by the fact that 6 of these 9 implausible colonists found congeners or close relatives already established on Vuatom (and would have found the same or similar competitors on almost any other Bismarck island of Vuatom's size and poverty). For instance, the sole vagrant individual of the high-*S* kingfisher *Ceyx websteri* that Father Meyer ever saw on Vuatom was being chased by the C-tramp kingfisher *Alcedo atthis*, which is established on Vuatom.

As striking as what Father Meyer saw is what he failed to see. Of the 127 species present on New Britain, only 4 miles over water from Vuatom, 55 were never observed by Father Meyer on Vuatom during his several decades there. These include 14 of New Britain's 15 montane species, 8 of the 9 fresh-water and marsh species, 32 of the 74 forest species, and 5 of the 18 species of grassland and open country, but all 10 of New Britain's aerial and sea-coast species were recorded. The lack of vagrants of montane and water species could be associated with the absence of these habitats on Vuatom. However, the 32 forest species (24 of them high-*S* species or A-tramps) had no such excuse for failing to appear as vagrants, and the conclusion is inescapable that attempted colonization even of suitable habitats across 4-mile water gaps must be a rare event for these species.

The patterns of relative dispersal ability derived from Long and from Vuatom are in general agreement, in indicating the high dispersal of supertramps and D-, C-, and B-tramps contrasted with the low dispersal of A-tramps and high-*S* species. However, there is a quantitative difference, in that dispersal of high-*S* species to Vuatom was not quite so negligible as it was to Long (7 vs. 1 species, respectively). Part of the explanation may be that Vuatom is much closer to New Britain than is Long (4 vs. 76 miles), and over-water dispersal of high-*S* species may fall off very steeply with distance. The other reason may be that the Vuatom high-*S* species records are mainly of vagrants observed over the course of three decades, whereas the Long records were obtained during two surveys lasting one month each and consisted largely of established populations. High-*S* species may have difficulty not only in dispersing but also in establishing new populations, because of low reproductive potential.

Supertramp dispersal.

In the case of the 13 supertramp species, dispersal rates are sufficiently high that instances may be observed even during a short residence in the Bismarcks. As summarized in Table 6, Umboi has only one resident supertramp species, but in 25 days on Umboi I observed vagrants of six others. Two additional supertramps breed on islets 2 miles from Umboi, and two more on an island 13 miles distant, so that frequent vagrants of these species are also expected. New Britain has no resident supertramps, but vagrants of six species have been recorded, and two more breed on islets a few hundred yards from New Britain and must also produce vagrants. These dispersing vagrants often prove to be juvenile birds.

Witnessed instances of over-water dispersal.

On five occasions in 1972, while surveying the islands to the west of New Britain, I observed birds dispersing over water from island to island while I was in a boat or on the coast. On July 14 two C-tramp swallows *Hirundo tahitica* left the coast of Sakar and flew at a height of 100–200 feet towards Umboi, 10 miles away, until they were lost to binocular view. On July 15, while I was on a boat one mile south of Sakar, a flock of 12 *Collocalia* swiftlets (either the D-tramp *vanikorensis* or the C-tramp *esculenta*) flew past me 50 feet over the water from the direction of New Britain towards Umboi, which is about 20 miles from New Britain at this point. On July 18 several flocks consisting of a dozen birds each of the supertramp pigeon *Ducula pistrinaria* were seen flying at a height of several thousand feet for at least 8 miles along the north coast of Umboi, heading in the direction of Tolokiwa 13 miles away. On August 6 a flock of seven *Ducula pistrinaria* took off from the coast of Crown, were joined half-a-mile offshore by an eighth bird, gained an altitude of about 1000 feet, and headed north-north-west, where there was no land in sight (and no land actually to be found until Manus, 200 miles distant). Within the first few miles the flock occasionally veered left or right by up to 90° for a fraction of a minute but never turned back towards Crown, and eventually disappeared from binocular view at a distance of 5–10 miles, still heading away from Crown. Finally, on August 12, while

Table 6. Dispersal and characteristics of supertramps

Species	Family	New Britain	Umboi	Food	Body weight (g)
Ptilinopus solomonesis	Columbidae	vagrant	resident	soft fruit	91
Ducula pistrinaria	Columbidae	vagrant	vagrant	soft fruit	470
Ducula pacifica	Columbidae	—	—	soft fruit	435
Ducula spilorrhoa	Columbidae	vagrant	vagrant	soft fruit	560
Macropygia mackinlayi	Columbidae	vagrant	vagrant	soft fruit	87
Caloenas nicobarica	Columbidae	vagrant	vagrant	hard fruit	635
Turdus poliocephalus	Turdinae	—	(13 miles)	insects, fruit	60
Monarcha cinerascens	Muscicapinae	(<1 mile)	vagrant	insects	26
Pachycephala melanura dahli	Pachycephalinae	vagrant	vagrant	insects	26
Aplonis feadensis	Sturnidae	—	—	fruit, insects	85
Myzomela pammelaena	Meliphagidae	(18 miles)	(3 miles)	nectar, insects	16
Myzomela sclateri	Meliphagidae	(<1 mile)	(13 miles)	insects, nectar	10
Zosterops griseotincta	Zosteropidae	—	(13 miles)	insects, fruit, nectar	14

Column 1 lists the 13 Bismarck supertramp species; column 2 gives the family; columns 3 and 4 indicate whether each species is resident on the species-rich islands of New Britain and Umboi, respectively; if not, whether it has been recorded as a vagrant; if not, whether it is resident on an island < 1, 3, 13, or 18 miles from New Britain or Umboi (hence likely to appear as a vagrant but to have been overlooked so far). A dash means that there are no records of vagrants and no resident population on an island within 18 miles. All of these supertramp species except *Ducula pacifica, Turdus,* and *Aplonis* occur on Long and Crown, and all except *Ducula pacifica, Aplonis,* and *Pachycephala* are on Tolokiwa. For each species, columns 5 and 6 give, respectively, the main components of the diet and the average body weight in grams.

in a boat halfway between Long and Tolokiwa (23 miles apart), I saw a flock of four of the A-tramp grass finch *Lonchura spectabilis,* flying 5–10 feet above the waves, heading straight from Long towards Tolokiwa in moderate wind, with rapid short wing-beats and an undulating, seemingly weak flight, progressing at about 14 miles/hour. I watched the flock from our boat for the next 10 minutes, at the end of which only three birds were left, still heading for Tolokiwa.

It is noteworthy that all five of these instances involved a flock of a normally gregarious species: if the target were reached, the chances of colonizing success would be higher for a flock arriving simultaneously than for separately dispersing individuals. It is also interesting that in four of the five instances the island towards which the colonists were heading was clearly visible at the height at which the colonists flew, and the colonists were heading straight for the target. Finally, unbeknownst to all five groups of colonists, a population of their species was already established on the target island (unless the swiftlets heading for Umboi were *Collocalia esculenta* rather than *C. vanikorensis*).

Rare dispersal events: gales and blooms.

The preceding five witnessed instances involve species that probably send out colonists frequently. However, the dispersal of other species depends on rare events, either gales or else a rare "bloom" of the species.

Between March 3 and 7, 1952, a gale blew pelicans *Pelecanus conspicillatus* from Queensland or New Guinea for several thousand miles over much of Melanesia (Bradley and Wolff, 1956). A flock of 20 reached Rennell; others reached Bougainville, Guadalcanal, San Cristobal, Santa Anna, Nissan, and many other islands in the Solomons, Feni in the Bismarcks, and various islands in the New Hebrides. Some of these colonists bred, and a population may still exist on Nissan. In June 1972 Cyclone Ida blew flocks of the parrot *Eos cardinalis* from the main chain of the Solomons 150 miles to the outlying atoll Ongtong Java, where the birds are now flourishing (Bayliss-Smith, 1973). The same cyclone brought a flock of the hornbill *Aceros plicatus* to Savo Island in the Solomons, and brought back the parrot *Geoffroyus simplex,* which had formerly been present on Savo but had disappeared. In the early 1960s a pair of the ibis *Threskiornis spinicollis,* moving north in Australia during a drought, were caught in strong winds and blown 1000 miles to New Ireland in the Bismarcks (Coates, 1973).

Occasionally an otherwise sedentary species experiences a "bloom" that disperses large numbers of individuals over a wide area. Father Meyer (1934) recorded blooms of the New Britain lowland forest pigeon *Ducula finschii* and montane forest pigeon *D. melanochroa* reaching Vuatom once in a period of three decades. He also recorded *D. melanochroa,* another montane forest pigeon *Gymnophaps albertisii,* and the lowland forest pigeon *Columba pallidiceps,* which are normally confined to the interior of New Britain, "blooming" at certain times on the coast. All of these pigeons are high-S species that occur on only a few Bismarck islands and probably colonize rarely. In the summer of 1875 a bloom of the Fijian Mountain Lorikeet *Vini amabilis* spread it widely over three Fijian islands (Mayr, 1945). In 1962, coincident with the seeding of mountain bamboo, two seed-eating birds, the A-tramp finch *Erythrura trichroa* and C-tramp pigeon *Gallicolumba beccarii,* became superabundant for a year in the Okapa Subdistrict of New Guinea. The last such bloom of these bird species and seeding of bamboo in this district had occurred several decades previously. In general, these blooms may reflect either colonists generated by a transient local superabundance of food, as in the last example, or else colonists expelled by a transient local failure of the normal food supply, as in the blooms of *Gymnophaps albertisii.* In either case, these blooms, like the rare dispersal events caused by gales, mean that even an ornithologist resident in an area for much of his lifetime may fail to observe directly the dispersal that is responsible for the long-term colonization potential of some species.

Relation Between Incidence Functions and Reproductive Rates

All other things being equal, good colonist species should have a high reproductive potential, so that propagules can fill up an island or recover from a population crash as quickly as possible. Otherwise, fluctuations in population size may wipe out the population at an early stage, when population size is still small. MacArthur and Wilson (1967, Chapter 4) showed that, for quick success in achieving carrying capacity, colonists should maximize the ratio $(\lambda - \mu)/\lambda = r/\lambda$, where λ and μ are the *per capita* birth rate and death rate, respectively. Crowell (1973) confirmed this prediction for rodents colonizing islands off the coast of Maine. One therefore expects this ratio to be maximal in the Bismarcks for supertramps, D- and C-tramps, and possibly for some other species of scarce lowland habitats. In the complete absence of knowledge of λ or μ for any Bismarck species, this expectation cannot be tested. However, we can at least examine whether colonizing ability is related to clutch size, number of broods per year, and length of breeding season, as tabulated for many Vuatom and New Britain species by Meyer (1930, 1933).

Most Bismarck species lay clutches of 1, 2, or 3, occasionally 4 or 5, eggs. No correlation is apparent between clutch size and type of incidence function, because a given clutch size is so characteristic of a given taxonomic group. For instance, clutch size is 1 in all except one Bismarck pigeon, 2 in myzomelid honeyeaters, 2 in *Monarcha* flycatchers, 3–4 in rails, and 3–5 in *Lonchura* finches, even though each group contains supertramps or tramps as well as high-S species. Of the seven supertramp species whose clutch size is known, four lay a single egg, while three lay 2 eggs. Clearly, superior colonists do not depend upon large clutches.

The Bismarcks lie near the equator, so that seasonal variation in daily hours of sunlight is negligible. However, each locality exhibits an idiosyncratic seasonal rainfall pattern. For example, the southern watershed of New Britain receives 80% of its rain in the months May–October, whereas the northern watershed receives 70% of its rain in the months December–April. Certain species concentrate their breeding activities in specific two-to-six-month periods of the seasonal cycle (e.g., most hawks in the dry season, the crow *Corvus orru* in the wet season, the kingfisher *Alcedo atthis* in the transition from wet season to dry season). Other species breed twice a year, each time at a specific stage in the rain cycle, generally at the transition from wet to dry season and again at the transition from dry to wet season. In the cases of still other species, breeding individuals can be found at any month of the year, and the same pair may rear several broods per year. For example, a pair of the D-tramp flycatcher *Rhipidura leucophrys* has been observed to raise six broods within six months (Mackay, 1970). The 22 Vuatom species known to breed throughout the year, or else to rear two or more broods per year, consist of 14 supertramps, D-tramps, or C-tramps; 3 A- or B-tramps of grassland or open country; and 5 A- or B-tramps of forest. The 16 Vuatom species known to have a single concentrated breeding season, and not known to rear multiple broods during this period, consist of 6 D- or C-tramps, 4 A- or B-tramps of grassland or open country, and 6 A- or B-tramps of forest. Supertramps and D- and C-tramps are definitely good colonists, A- and B-tramps of forest are definitely poorer colonists, and A- and B-tramps of grassland and open country may be either good colonists whose distribution is limited by habitat availability, or poorer colonists. All five supertramps studied breed year-round, and two of them are known to rear two or more broods. Thus, the ratio of year-round breeders and/or multiple-brooded species to single-brooded seasonal breeders is higher among definitely good colonists $(^{14}/_{6} = 2.3)$ than among definitely poor colonists $(^{5}/_{6} = 0.8)$.

In other words, many but not all good colonists have higher-than-average per capita birth rates λ. A perfect correlation is not expected, since colonist success depends on the ratio $(\lambda - \mu)/\lambda$, not just on λ, and it may be easier to maximize this ratio by decreasing μ than by increasing λ. For example, the three D-tramp large hawks of the Bismarcks (the eagle *Haliaeetus leucogaster,* osprey *Pandion haliaetus,* kite *Haliastur indus*) have low birth rates (single-brooded seasonal breeders, one or two eggs per clutch) but disperse over water very readily and are probably long-lived (low μ).

The Supertramp Strategy Versus the Overexploitation Ethic

Ornithologists who have observed mainly on New Britain are accustomed to thinking of the supertramps as habitat specialists, confined to small coral islets off the New Britain coast. A visit to Long, a large (173 square miles) and high (4300 feet) island defaunated by an eruption two centuries ago, shows how misleading this impression is. Eight of the ten supertramp species of Long are abundant in literally every land habitat with low or high trees: in strand forest, open savanna, coconut groves, gardens, tall forest of the hill slopes, a closed-canopy forest without understory or middle-story foliage on the crater rim, montane cloud forest, and dense elfin forest or subalpine shrubbery at the highest elevations; in bright sunlight, in forest shade, or in virtually permanent cloud cover; in the dryness of the coast, where for four months there is no rain and only a few fresh-water springs, or in the perpetual moisture and mists of the cloud forest; in the heat at sea level, or in the cold of the summits. Similarly, seven of the ten supertramps of Tolokiwa, an extinct volcano near Long, are abundant from sea level to the cloud forest on the summit at 4650 feet. On Karkar two of the five supertramps occur from sea-level up to cloud forest around 5000 feet, and one occurs through subalpine shrubbery to the summit at 6000 feet, where it is the sole bird species. Thus, if supertramps occur on an island at all, they are extraordinarily catholic in their habitat tolerance.

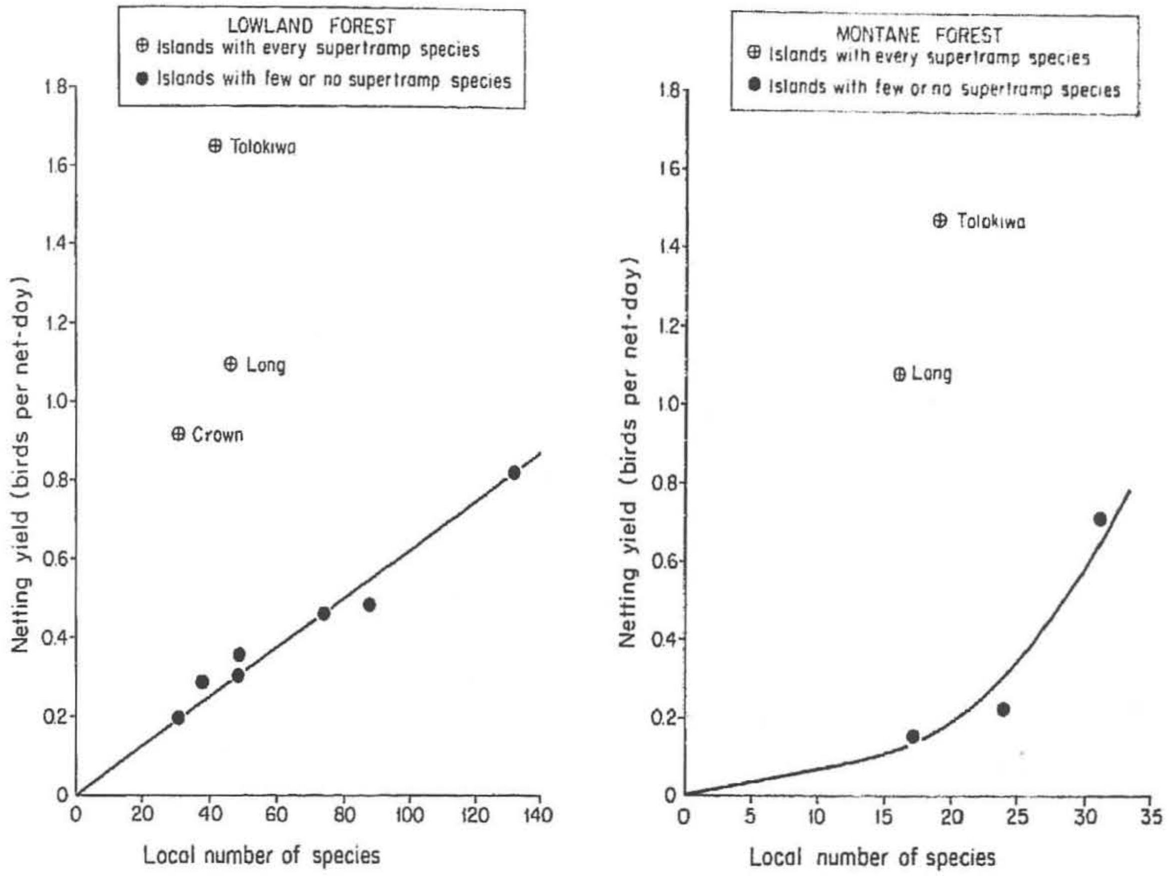
Supertramps are virtually absent as residents on the species-rich, large, central islands of the Bismarcks (New Britain, New Ireland, New Hanover, Umboi). With one set of exceptions, the islands that have more than four resident supertramp species are either small (less than 6 square miles), or isolated by a water gap of at least 50 miles from the large central islands, or both. The set of exceptions is particularly striking in that it constitutes the most supertramp-rich islands of the Bismarcks: Long, Tolokiwa, and Crown, with ten species of supertramps each. Long is large and close (37 miles) to the species-rich central island Umboi, and Tolokiwa and Crown are the two islands nearest Long. The obvious reason for the presence of so many supertramps on Long is that, by virtue of their rapid dispersal and breeding, they were the first species to arrive and become reestablished after the recent volcanic holocaust. Tolokiwa and Crown, as the nearest neighbors of Long, and with respective areas only 10% and 3% of Long's, have been the most immediate and visible targets for birds dispersing from the supertramp breeding vat on Long and must have been inundated by supertramp colonists. Most of the other species of Tolokiwa, Crown, and Long are D- and C-tramps.

The strategy of the supertramps may be summarized as "Breed, disperse, tolerate anything, specialize in nothing." They represent the extreme of *r*-selected species (cf. discussions by Shapiro, Chapter 8, and Patrick, Chapter 15). In this respect supertramps resemble the species that have been variously called "fugitive species," "opportunistic species," "weeds," or "tramps." The difference is that supertramps are virtually confined to small islands, where they occur in practically any habitat, whereas fugitive species also occupy or are characteristic of unstable habitats on large islands. The investment of supertramps in reproduction and in dispersal powers presumably comes at the expense of competitive ability and harvesting efficiency. On species-rich islands the supertramps are outcompeted and permanently excluded by guilds of *K*-selected high-*S* specialists, each of which is better adapted to some fraction of the supertramps' potential niche. For example, on New Britain or New Ireland the supertramp fruit dove *Ptilinopus solomonensis* is replaced by three congeners, one confined to mountains, another to lowland forest, a third to open lowland habitats; the medium-sized supertramp fruit pigeon *Ducula pistrinaria* is excluded by three congeners, one large species and one small species in the lowlands, a third in the mountains; the supertramp cuckoo-dove *Macropygia mackinlayi* is replaced by three cuckoo-doves that form a graded size series; and the supertramp flycatcher *Monarcha cinerascens* is replaced by four related flycatchers, one in the mountains, a second in lowland second-growth, a third in the canopy of lowland forest, and a fourth in the interior of lowland forest. On small islands, where extinction rates are high, only the supertramps can recolonize frequently enough to have a high incidence. On larger islands defaunated by volcanic activity or tidal waves, the supertramps are first to arrive and rapidly fill the island. By the time the more slowly dispersing specialists follow and crowd out the populations of supertramps, the latter have already found another defaunated island and thereby ensured their survival as a species. With the explosion of a large island like Long, the supertramps "struck it rich" as first arrivals. For some supertramp species the colonization of Long quadrupled the population of the whole species.

To an observer who comes to the supertramp-rich islands Long, Tolokiwa, or Crown from a "normal" island, the feature of these islands that becomes most obvious within the first hour of field observations is the extraordinary abundance of birds. As quantitated by mist-net techniques (Figure 18), population densities of all species combined are up to six times higher in lowland forest, and up to nine times higher in montane cloud forest, on the supertramp-rich islands than on "normal" control islands with the same number of species. These excess densities are largely due to the abundance of the supertramps themselves, which account for 40–70% of all bird individuals in lowland forest of these three islands, and 73–90% of all bird individuals in montane cloud forest.

Several possible explanations that immediately come to mind for these startlingly high abundances do not withstand scrutiny. Could bird populations on "normal" islands be kept below carrying capacity by predators (as is true for many of the species discussed by Connell in Chapter 16), so that supertramp abundance represents a release from predation pressure? In fact, predators of birds on Long (two species of falcon, an eagle, and the nest-robbing marsupial *Phalanger orientalis*) are at least as diverse as on normal islands, and far more numerous, mainly because of the abundance of the marsupial that has struck every visitor to Long. Could supertramps be taking over the niches of lizards, mammals, or some other nonavian competitors that are present on normal islands but unable to reach Long? Long in fact has small and large lizards, frogs, rats, the phalanger, and insectivorous, nectar-feeding, and frugivorous bats; and the supertramps include omnivores, insectivores, nectar-feeders, and specialists on soft or hard fruit, and cover a wide range of sizes (Table 6). Could the supertramps be drawn disproportionately from small species, so that the excess abundance of individuals does not reflect an excess biomass? In fact, there is little difference between supertramp-rich islands and normal islands in the average weight of a netted bird. Could mist-netting techniques greatly overestimate the abundance of supertramps? The netting results are at least qualitatively confirmed by field impressions of obvious abundance. Furthermore, more individuals were netted of the territorial than the nonterritorial supertramp species (the latter happen to be species that forage largely above the height of the nets), so that wanderings of nonterritorial supertramps are unlikely to have significantly inflated the mist-net yields. Could excess abundances on Long, Crown, and Tolokiwa reflect high productivity of rich volcanic soil resulting from ash fall-out during the Long explosion? But Tolokiwa received little ash from the Long explosion.

Rather, the high densities of birds on Long, Crown, and Tolokiwa must be a property of the supertramp-rich communities themselves, since physically similar volcanic islands that are more distant



(a) (b)

Figure 18 Ordinate: rate of catching land birds under standardized conditions in mist nets on a given island (expressed in birds caught per net-day), in lowland forest (Figure 18a, left) or montane cloud forest (Figure 18b, right). Abscissa: local number of species present on the island. If one compares the same type of habitat on different islands (but not if one compares different habitats), this catch rate is proportional to the combined population densities of all species present (Diamond, 1970b). Symbols: ●, control islands with not more than three supertramp species; ⊕, the exploded volcano of Long and two control islands, which support ten supertramp species each. Note that, on islands with few supertramps, netting yields (and total population densities) increase with the local number of species (as interpreted by Diamond, 1970b); and that the islands with many supertramp species have much higher yields than islands with the same total number of species but few supertramps. (From Diamond, Copyright 1974 by the American Association for the Advancement of Science.)

from Long and were not inundated by supertramps do not have the excess population densities. This interpretation is confirmed by the situation on the mountainous island Karkar, where spatially separate supertramp-rich and supertramp-poor communities with very different population densities contrast within the same island. On Karkar and the adjacent lower island of Bagabag, supertramps constitute a considerable minority of species in all major bird guilds except at high elevations on Karkar, where the supertramp honeyeater *Myzomela sclateri* is the sole species in the insectivorous gleaner guild. Below 4000 feet *Myzomela sclateri* is excluded by two sunbird species, and in subalpine shrubbery above 5000 feet there is no other bird species at all besides this supertramp. In lowland forest on Karkar (third-from-left-most solid point, Figure 18a) and Bagabag (left-most solid point, Figure 18a), and in montane forest below 4000 feet on Karkar (left-most solid point, Figure 18b), total population densities measured by mist-netting fall on the curve for "normal" islands. At the highest elevations on Karkar, however, *Myzomela sclateri* was obviously much more abundant than all bird species combined in similar habitats on supertramp-poor islands I have studied, although no mist-netting was done to quantify this finding.

At first, it seems paradoxical that supertramp guilds, where they are present, maintain much higher population densities than the high-S competitors that exclude them from most islands. If one thinks of the high-S species as K-selected, then K-selected guilds have much *lower* equilibrium abundances than do supertramp guilds, and the term K-selection becomes misleading and contradictory. However, as MacArthur predicted (1972, p. 31), "self-renewing resources can be overexploited to the detriment of the predator's population, and this overexploitation will be a natural consequence of competition among the predator species." That is, competition in a high-S fauna selects for those species that can reduce resource levels below the point where other species can survive, even though this diminishes the rate of resource production and hence the population density of harvesting species (see MacArthur, 1972, pp. 56–57 for a simple model). For example, high-S guilds of insectivorous birds, by catching insects more efficiently than do supertramps, may be depressing sustainable insect yields far below the level that exists on supertramp-rich islands. In the most species-rich community on earth, the neotropical rainforest, Elton (1972) has already emphasized the low total *densities* (despite high diversity) of insects, and the relation of these low prey densities to sustained predator pressure. The mechanism of fruit overexploitation by high-S frugivores must differ from the mechanism among insectivores, since the number of fruits produced is independent of the harvest rate so long as the reseeding of new fruit trees is not suppressed. What may be happening is that high-S frugivores are selected by competition to harvest the fruit at an earlier stage of ripeness than supertramps can tolerate, thereby eliminating the supertramps but also reducing the energy yield available to the remaining species from eating less ripe or smaller fruit.

Thus, the supertramp strategy may be contrasted with the overexploitation ethic forced on high-*S* faunas by competition: "Harvest early, overexploit, and starve out the next species, lest the next species harvest earlier and closer." The overexploitation ethic adopted by high-*S* species under the pressure of interspecific competition, and to the detriment of their own population densities, strikingly exemplifies the conclusion reached by Levins in Chapter 1, that the course of natural selection in a particular species may not be comprehensible without reference to the whole matrix of community interactions. Lowering of resource levels, whether by a single species or by a mutually adjusted guild of species, may be the principal mechanism by which invaders are competitively excluded from integrated communities. If these interpretations are correct, they imply that predators in high-*S* communities have a major impact on the densities of their prey. Later in this chapter we shall apply Levins's method of loop analysis to determining the conditions under which overexploitation is a useful strategy for its practitioners.

In the remainder of this chapter we shall search for evidence that local species guilds are in fact composed of coadjusted species and do resist invaders. A lesson to draw from our discussion of incidence functions is that the clearest evidence is likely to come from exclusion of supertramps by other species. The catholic habitat tolerance of most supertramps means that they are capable of thriving on virtually any island of the southwest Pacific. Because of the demonstrated high dispersal of at least some of the Bismarck supertramps, we can assume that every island of the Bismarcks is continuously bombarded by their colonists, and we can reasonably conclude that absences of supertramps from islands are due to competitive exclusion.

The Meaning of Assembly Rules

In the section "Relations between incidence functions and island area" we considered reasons why the incidence *J* of a given species should in general increase with island area, or why the total number of species *S* should increase with island area. For most species *J* has to be and is an increasing function of *S*. There are also obvious reasons why the function should not be identical for all such species. The form of the function depends, for instance, on each species' preferred habitat type, minimum territory requirement, patchiness of food supply, magnitude of population fluctuations, dispersal ability, and birth and death rates. In discussing incidence functions so far, we have hardly mentioned interspecific competition or coadjustment of species. Does competition fail to contribute to the form of $J(S)$? Do the properties of each species considered individually tell us most of what we need to know in order to predict how communities are assembled from the total species pool? Note, for instance, that only if all species had the same incidence functions would one expect communities to contain random samples of the species pool. Since properties of individual species already lead us to expect incidence functions of different shapes (though usually increasing functions of S), we expect even communities of noncompeting species to appear as if they are assembled in nonrandom ways. Are all the rules for community assembly contained in the incidence functions?

There are three clear indications that the answer to these questions is "No." We have already seen one type of evidence that competition affects the form of $J(S)$, and that there must exist some assembly rules besides "incidence rules" (i.e., besides constraints that can be deduced from incidence functions alone): evidence derived from supertramps. For these species J does not approach 1.0 with increasing S but instead goes to zero at some upper S_{crit}. Naturally, this does not mean that a dispersing juvenile supertramp flies into an island, performs a quick avifaunal census, and flies off if he sees that some preprogrammed upper S_{crit} is exceeded. Naturally too, we should not suppose that all species have equally detrimental effects on a supertramp, and that when a certain species number has been exceeded, the combined effect of all the species outcompetes or starves out the supertramp. Instead, the supertramp is outcompeted or starved out by the combined effects of those species that harvest similar resources, the other species in the supertramp's guild. Since the number of these guild species increases with S just as does the number of species in any arbitrary subset of the species pool not biased towards supertramps, the incidence of the supertramp is seen to decrease at high S. Evidently the supertramp can fit into only certain small subsets of his guild. The problem thus becomes one of determining exactly which of the species that are being recruited into communities with increasing S are responsible for excluding the supertramp, and to what extent and in what combinations.

A second clear indication of competitive effects on $J(S)$ is provided by changes in $J(S)$ as a function of the species pool. Although each of the three island archipelagoes of Melanesia (Bismarcks, Solomons, and New Hebrides) supports a somewhat different species pool, many bird species of the Bismarcks occur in the other two archipelagoes. In an archipelago where a species finds fewer competing guild members in the species pool, the incidence category of that species shifts from supertramp towards D- or C-tramp, or from high-S species towards D-tramp. For example, in the Bismarcks the cuckoo-dove *Macropygia mackinlayi* belongs to a guild of four species and is a supertramp, absent from the largest islands (Figure 6 below). The total species pool of the Solomons is approximately as large as that of the Bismarcks, but only one other cuckoo-dove species occurs in the Solomons besides *Macropygia mackinlayi,* which becomes a D-tramp (Figure 19), present on the largest islands as well as on smaller islands. *Macropygia mackinlayi* is also a D-tramp in the New Hebrides, where there is no other cuckoo-dove. Similarly, *Ptilinopus solomonensis,* a supertramp in the Bismarcks, is present on large islands of the Solomons; and the Bismarck supertramps *Ducula pacifica* and *Turdus poliocephalus* become C-

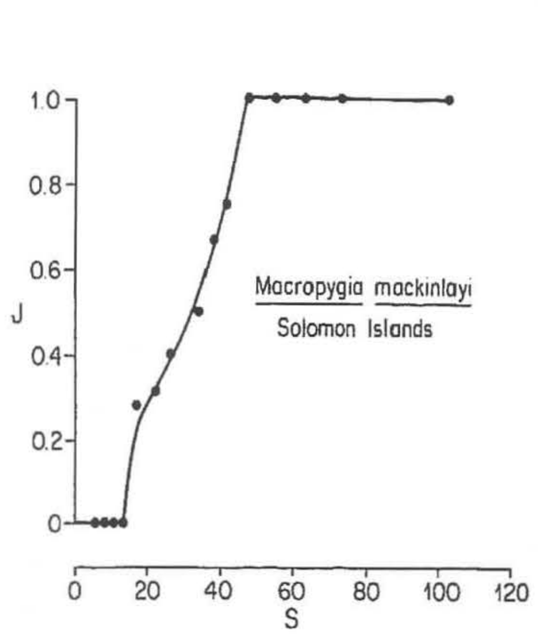


Figure 19 Incidence function for the cuckoo-dove *Macropygia mackinlayi* in the Solomon Islands, where only one other species of cuckoo-dove is present and *M. mackinlayi* is a D-tramp. Compare Figure 6 below, the incidence function for this species in the Bismarck Archipelago, where three other cuckoo-dove species occur and *M. mackinlayi* is a supertramp, excluded from the largest islands by competing congeners.

tramps in the poorer species pool of the New Hebrides, where they occur on large as well as small islands. Thus, the exclusion of supertramps from large islands is due to the presence of competing species in the same archipelago. Conversely, the Bismarck A-tramp rail *Porphyrio porphyrio* and B-tramp flycatcher *Pachycephala pectoralis* become C-tramps in the New Hebrides, where there are fewer competing species of rails and flycatchers. Thus, the absences of these species from some small Bismarck islands, like the absences of the supertramps from all large Bismarck islands, involve effects of competitors.

The other type of unequivocal evidence for additional assembly rules besides incidence rules comes from competitive exclusion patterns. Occasionally one finds two closely related species that occur in a checkerboard distribution pattern without ever coexisting. This would not be predicted from the incidence functions of the two species unless the ranges of S values over which J was nonzero were nonoverlapping, and such nonoverlap of $J(S)$ is rarely the case for species with checkerboard distributions (cf. *Pachycephala pectoralis* and *P. melanura dahli* in Figure 28, *Macropygia mackinlayi* and *M. nigrirostris* in Figure 25, and *Myzomela sclateri* and *M. cruentata* in Figure 29). There are also more complex cases in which combinations of more than two species, the feasibility of whose existence is compatible with incidence functions, never exist. This evidence also indicates that there are constraints on how species fit together besides the constraints implicit in incidence functions.

To understand the role of competition in the assembly of communities, we shall begin with the most clearly illustrative but least important example, the distributional checkerboard. We shall then go through more complicated but still decipherable examples from four guilds that illustrate *diffuse competition*, the phenomenon of a species that is unable to fit into a community because it is excluded by specific *combinations* of other species.

"Simple" Checkerboard Distributions: the Dilemma of the Empty Squares

If we suppose that stable communities consist of coadjusted species that exclude invaders by competition, the simplest distributional pattern that might be sought as possible evidence for competitive exclusion is a checkerboard distribution. In such a pattern, two or more ecologically similar species have mutually exclusive but interdigitating distributions in an archipelago, each island supporting only one species. An increasing number of instances of such checkerboard distributions have been reported in the recent literature (cf. Stresemann, 1939, for the islands of Indonesia; Mayr, 1942, for islands of the southwest Pacific; Lack, 1971, for islands of the West Indies; MacArthur, Diamond, and Karr, 1972, for Panamanian islands; Diamond, 1972a, for habitat islands on New Guinea). Figures 20–24 illustrate five examples from the southwest Pacific. Figure 20 involves two species of *Macropygia* cuckoo-doves in the Bismarcks; Figure 21, two species of *Pachycephala* whistlers in the Bismarcks; Figure 22, two species of *Ptilinopus* fruit doves in the Bismarcks; Figure 23, five species of small *Myzomela*

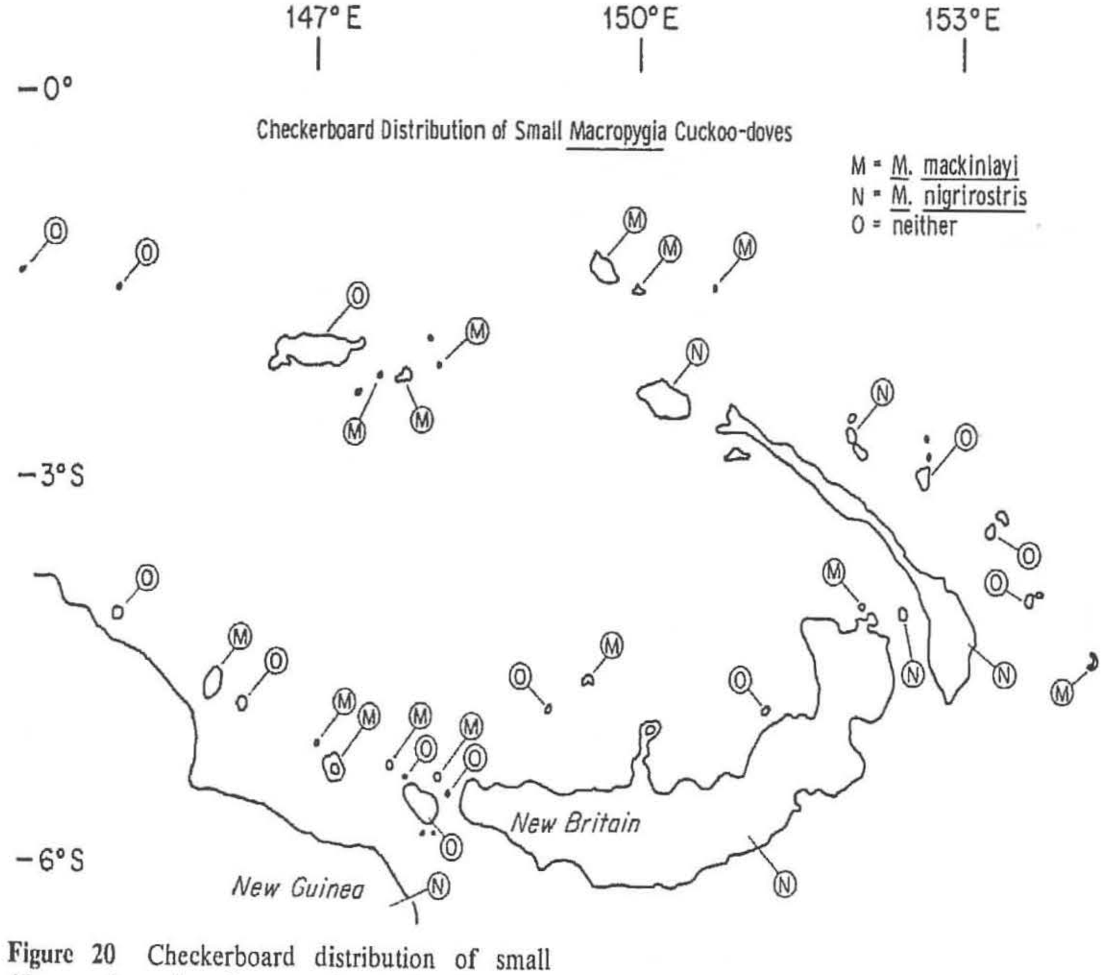


Figure 20 Checkerboard distribution of small *Macropygia* cuckoo-dove species in the Bismarck region. Islands whose pigeon faunas are known are designated by *M* (*Macropygia mackinlayi* resident), *N* (*Macropygia nigrirostris* resident), or 0 (neither of these two species resident). Note that most islands have one of these two species, no island has both, and some islands have neither.

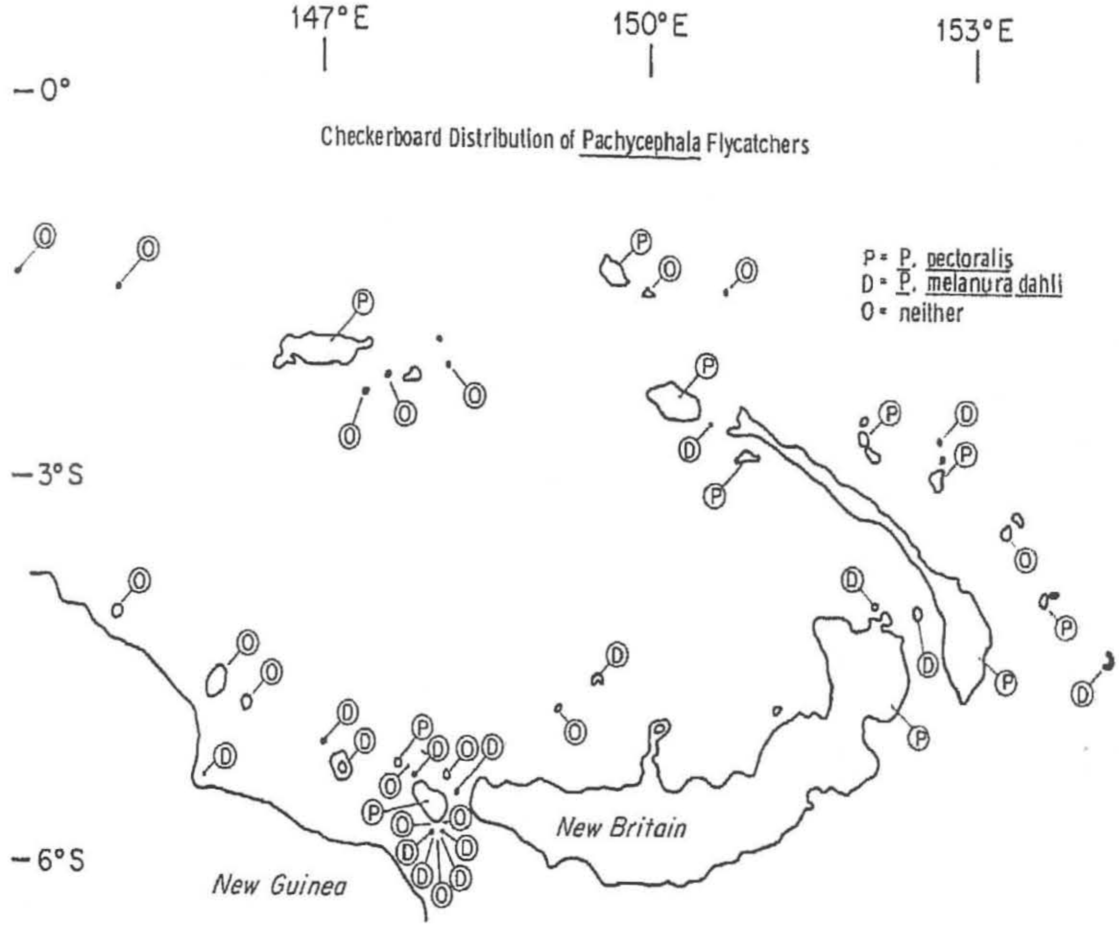


Figure 21 Checkerboard distribution of *Pachycephala* flycatcher species in the Bismarck region. Islands whose flycatcher faunas are known are designated by *P* (*Pachycephala pectoralis* resident), *D* (*Pachycephala melanura dahli* resident), or 0 (neither of these two species resident). Note that most islands have one of these two species, no island has both, and some islands have neither.

honeyeaters in the Bismarcks; and Figure 24, 12 species of *Zosterops* white-eyes in the Moluccas, New Guinea region, and Bismarcks. In each instance, an island supports only one species of the pair or group, but the distributions of the locally successful colonists replace each other in a checkerboard-like, irregular, geographical array. On each island the identity of the locally successful colonist may have been determined either on a first-come-first-served basis, or on the basis of slight competitive advantages related to slight ecological differences among islands (see section on "Chance or Predestination?"). Once established, one species would be able to exclude its relatives indefinitely or at least for a long time.

Figures 20–24 also illustrate a complication that has generally been glossed over in discussions of checkerboard distributions. In every figure, it is not sim-

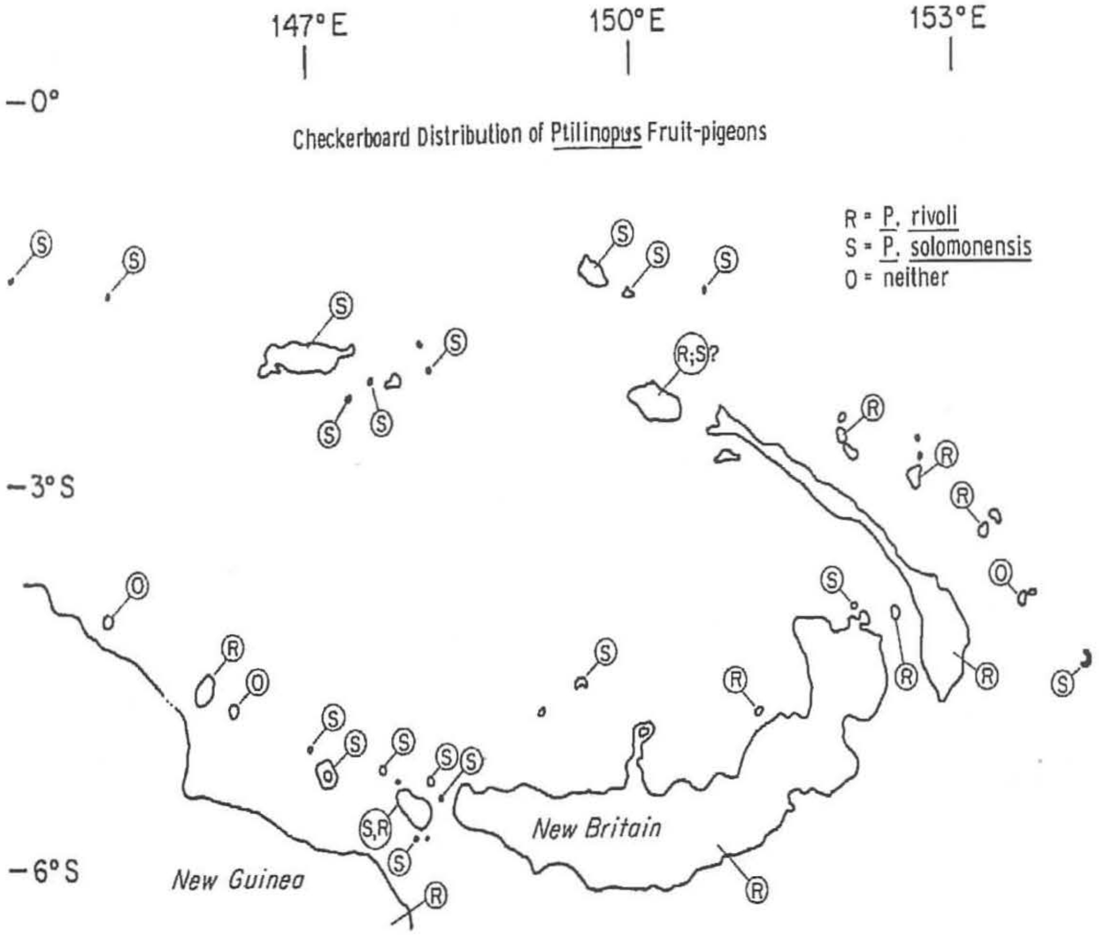


Figure 22 Checkerboard distribution of two closely related fruit pigeons in the Bismarcks. Islands whose pigeon faunas are known are designated by *R* (*Ptilinopus rivoli* resident), *S* (*Ptilinopus solomonensis* resident), or 0 (neither of these two species resident). Note that most islands have one of these two species, only one or perhaps two islands have both, and only a few islands have neither.

ply that each island supports one member of a group, no more and no less: some islands support no member at all. For instance, 11 Bismarck islands support *Pachycephala pectoralis,* 18 support *Pachycephala melanura dahli,* and 21 support neither. One might be tempted to explain the vacant islands by postulating that they are unsuitable for either species, or that by chance neither species has arrived, or that some empty islands are inevitably expected in the low-*S* portion of incidence curves, or that some other related species has been overlooked and fills the vacant islands. However, none of these explanations is plausible for the cases illustrated in Figures 20–24. In each of these five examples, at least one of the vicariant species is a supertramp of catholic habitat tolerance and high dispersal ability, so that it undoubtedly has sent colonists to the vacant islands and does exist elsewhere in physical environments similar to those left vacant. The vacant islands do have other species not depicted in Figures 20–24, which are ecologically similar to the supertramp, although not as similar as the strictly vicariant species. However, in each case some islands can be found on which the supertramp coexists with each of the other related species. For instance, in addition to the similar-sized small cuckoo-doves *Macropygia nigrirostris* and *M. mackinlayi* of Figure 20, there are two larger species, *M. amboinensis* and the *Reinwardtoena* su-

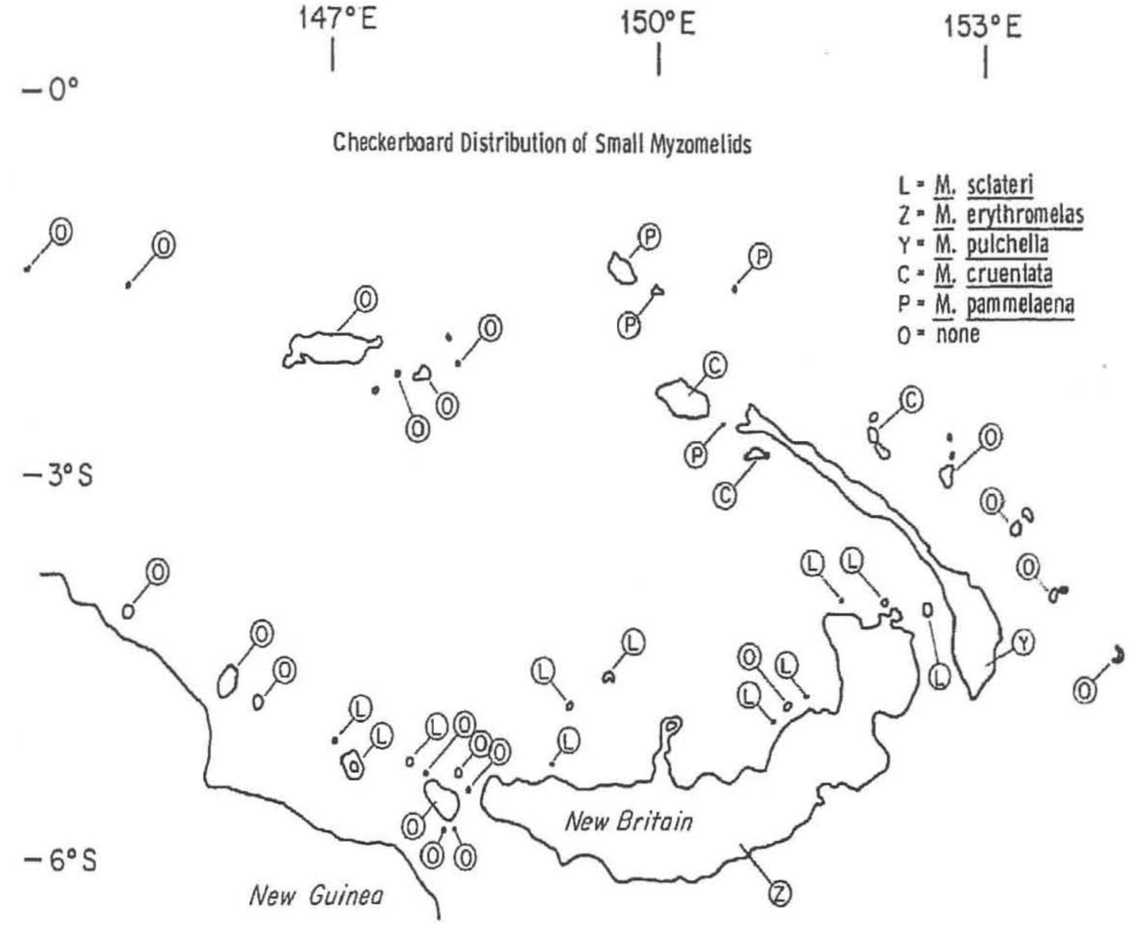


Figure 23 Checkerboard distribution of small myzomelid honeyeaters in the lowlands of Bismarck islands. Islands are designated by *L* (*Myzomela sclateri* resident), *Z* (*Myzomela erythromelas*), *Y* (*Myzomela pulchella*), *C* (*Myzomela cruentata*), *P* (small-sized races of *Myzomela pammelaena;* there are additional large-sized races in the northwest Bismarcks and on Long and its neighbors), or 0 (none of these species resident). Note that half of the islands have one lowland myzomelid species, no island has two species, and half of the islands have none. The two largest islands have an additional species in the mountains.

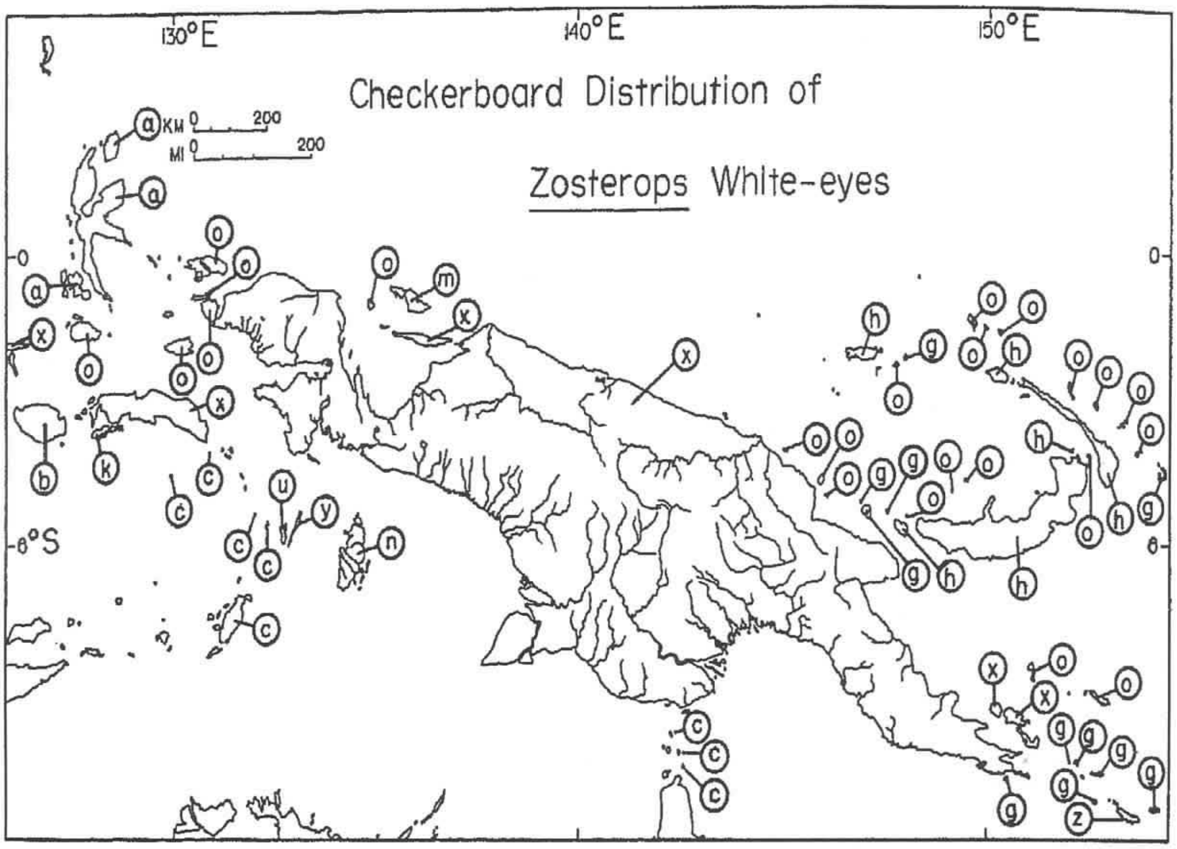


Figure 24 Checkerboard distribution of twelve white-eyes in lowland and/or hill forest of islands of the New Guinea region. Islands are designated by *a* (*Zosterops atriceps*), *b* (*Z. buruensis*), *c* (*Z. chloris*), *g* (*Z. griseotincta*), *h* (*Z. hypoxantha*), *k* (*Z. kuehni*), *m* (*Z. mysorensis*), *n* (*Z. novaeguineae*), *u* (*Z. uropygialis*), *x* (*Z. atrifrons*), *y* (*Z. grayi*), *z* (*Z. meeki*), or 0 (no species). Five of the largest islands have an additional species in the mountains. Species *a, h, m, x,* and *z* belong to a superspecies.

perspecies. Each island left vacant both by *M. nigrirostris* and *M. mackinlayi* does have either *M. amboinensis* or *Reinwardtoena* or both. However, numerous islands can be found as illustrations of the ability of *M. nigrirostris* to coexist with either of the two larger species, and similarly for *M. mackinlayi*. Thus, no other species can be found to fill the vacant islands of the Figure 20 checkerboard on a one-species-per-island basis. In Figures 21–24 as well, one-to-one competitive exclusion fails to explain why the checkerboards have numerous empty squares.

Checkerboard distributions are of great interest in demonstrating the existence of competitive exclusion. Nevertheless, the complication of the empty squares shows that there is no distributional pattern in the Bismarcks that can be understood completely in terms of one-to-one competition. In addition, there is a far more serious difficulty in trying to understand community resistance to invasion in terms of one-to-one competition: the distributions of only a few species can be understood even partly on this basis. For most Bismarck species one cannot point to any close relative with which it is unable to coexist: most pairs of close relatives are demonstrably compatible on one or another island. Thus, the innumerable instances of vagile species excluded from physically suitable islands—instances that are implicit in the $J < 1$ region of many incidence functions—must have a more complex explanation than one-to-one competitive exclusion.

Assembly Rules for the Cuckoo-Dove Guild

Let us consider the cuckoo-dove guild in detail, because it is the only Bismarck guild for which the assembly rules can at present be deduced completely, and because there is considerable historical evidence that permissible combinations of species do resist forbidden invaders.

Cuckoo-doves are a group of arboreal, long-tailed, fruit-eating pigeons that live in the middle story of shaded forest from India east to Melanesia. In the eastern portion of this region, from the Moluccas to the New Hebrides, occur four species or superspecies: the *Reinwardtoena* superspecies, which is large (weight, average 297 g, range 279–315); *Macropygia amboinensis,* which is medium-sized (149 g, range 128–178); and *M. mackinlayi* (87 g, range 73–110) and *M. nigrirostris* (86 g, range 73–97), which are smaller. As with other guilds in which successive members differ by a factor of 2 in weight (Diamond, 1972a, pp. 43–44; Figures 30 and 31 of this chapter; see also Brown, Chapter 13, Figures 5 and 6, and Hespenheide, Chapter 7, Figure 4), ecological segregation among sympatric cuckoo-doves depends on the fact that larger species can eat larger fruits, but smaller species can perch on lighter twigs and perches. All four species coexist in the Bismarcks. To the east, only *Reinwardtoena* and *mackinlayi* occur in the Solomons, and only *mackinlayi* in the New Hebrides. To the west, New Guinea has three species (*mackinlayi* absent), and the Moluccas have *Reinwardtoena* and *amboinensis.* The two most similar species in phylogeny and in size are *nigrirostris* and *mackinlayi,* which are products of a recent speciation, largely allopatric, and overlap only in the Bismarcks.

Figure 25 compares the incidence functions of the four species in the Bismarcks. *M. nigrirostris* is an A-tramp, *Reinwardtoena* a B-tramp, *amboinensis* a C-tramp, and *mackinlayi* a supertramp.

Figure 26 plots the number of cuckoo-dove species on each Bismarck island as a function of total species number on the island. Only some of the poorest islands ($S \leq 18$) lack cuckoo-doves, and all islands with $S \geq 20$ have one or more species. Islands with $S = 9$–47, 20–83, and 62–127 have 1, 2, and 3 cuckoo-dove species, respectively.

Cuckoo-dove species are able to coexist on a single island only in certain combinations. Table 7 summarizes "permitted combinations" and "forbidden combina-

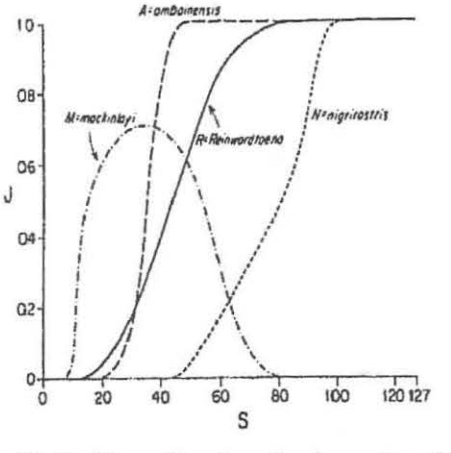


Figure 25 Incidence functions for the cuckoo-doves *Macropygia mackinlayi*, *M. amboinensis*, *M. nigrirostris*, and *Reinwardtoena browni* in the Bismarcks.

tions," i.e., combinations that occur on many islands, as opposed to combinations that occur on no island. Two of the four possible one-species combinations, three of the six possible two-species combinations, three of the four possible three-species combinations, and the sole possible four-species combination are forbidden. In the cuckoo-dove guild, as in other guilds, it turns out empirically that combinations may be forbidden on the basis of any one of three types of rules, which we shall term incidence rules, compatibility rules, and combination rules. In the following discussion we symbolize the four cuckoo-doves as A = *amboinensis*, M = *mackinlayi*, N = *nigrirostris*, and R = *Reinwardtoena*.

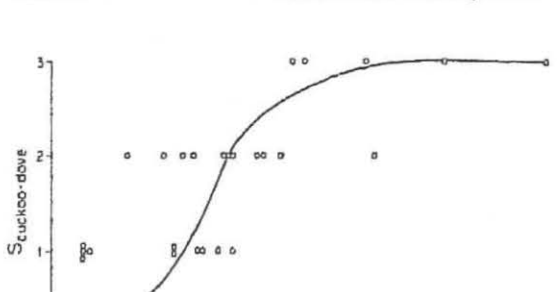


Figure 26 Number of resident species of cuckoo-doves on each Bismarck island (ordinate), as a function of the total number of resident bird species on the island (abscissa). The solid curve is drawn through points at the average value of S_{total} for each $S_{\text{cuckoo-dove}}$ value.

Incidence rules.

Examination of incidence functions alone tells us, without need for any further information, that certain combinations cannot occur. Thus, Figure 25 shows that J_A equals 1.0 (where J_A symbolizes the incidence of *amboinensis*) for all S exceeding the lower S_{crit} for *nigrirostris*, the S value below which $J_N = 0$. That is, all islands that have *nigrirostris* also have *amboinensis*. We therefore know that any combinations containing N but not A—i.e., the combinations N, NR, MN, and MNR—are forbidden. We shall use the term "incidence rules" to refer to constraints on species assembly that follow immediately from incidence functions.

Compatibility rules.

Distributional information combined with knowledge about species ecologies may suggest to us that a given pair of species is incapable of coexistence on an island under any circumstances, either alone as a pair, or as part of a larger combination. Absolute incompatibility is likely to be encountered only between two species that are products of a recent speciation and so similar ecologically that they cannot occupy the same space. An example is provided by the cuckoo-doves *M. mackinlayi* and *M. nigrirostris*, which must have constituted a superspecies until a relatively recent reinvasion of the Bismarcks brought them into contact. These

Table 7. Assembly rules for the cuckoo-dove guild

Number of species	Assembly observed	Permitted combination	Forbidden combination	Collapse observed	Reason why forbidden
1		A (3,13)			
	$—, + M\rightarrow$	M (8,41)			
			N		incidence
			R		combination
2	$M, + A\rightarrow$	AM (5,0)			
		AR (4,15)			
		MR (2,12)			
			AN		combination
			MN		compatibility and incidence
			NR		incidence
3		ANR (5,4)			
			AMN	$AM + N\rightarrow\mid$	compatibility
			AMR	$AM + R\rightarrow\mid$, $AR + M\rightarrow\mid$	combination
			MNR	$MR + N\rightarrow\mid$	compatibility and incidence
4			$AMNR$	$ANR + M\rightarrow\mid$	compatibility

For all possible 1-species, 2-species, 3-species, and 4-species combinations of the four cuckoo-dove species (A = *Macropygia amboinensis*, M = *Macropygia mackinlayi*, N = *Macropygia nigrirostris*, R = *Reinwardtoena* superspecies), the table indicates whether the combination does occur ("permitted combination") or never occurs ("forbidden combination") on islands. The two numbers after each permitted combination give, respectively the number of Bismarck islands, and the number of islands outside the Bismarcks (Moluccas, Papuan islands, Solomons, New Hebrides), on which the combination is resident. "Assembly observed" indicates cases in which assembly of a permitted combination has been observed historically, when the second-named species (named after the plus sign) has successfully invaded a community of the first-named species (named before the plus sign; the dash in the second row indicates that no cuckoo-dove was present before species M invaded). "Collapse observed" indicates cases in which collapse of a forbidden combination has been observed historically, when the second-named species has unsuccessfully invaded a community of the first-named combination (e.g., in the last row, the entry means that invasions of ANR by M have been observed and have been unsuccessful). The last column gives the type of assembly rule that disallows each forbidden combination.

species are of the same size, coexist on no island, are similar ecologically, and differ mainly in distributional strategy (supertramp vs. A-tramp). Thus, the combinations *MN* as well as *MNR, AMN,* and *AMNR* are forbidden by "compatibility rules." The first two of these combinations are also forbidden by incidence rules.

If *mackinlayi* and *nigrirostris* were not incompatible, their highest probability of coexistence would be on islands with $53 \leq S \leq 66$, where the product $J_M J_N$ exceeds 0.04, reaching a maximal value of 0.06 at $S = 58$. However, there are only six Bismarck islands in this S range whose resident cuckoo-doves are well known. In general, the probability $p_{i,ab}(S)$ of *not* observing two species a and b together, whether as ab or as part of a larger combination, on an island i of species number S_i is given by

$$p_{i,ab}(S_i) = 1 - J_a(S_i)J_b(S_i) \qquad (4)$$

Then the no-coexistence probability Z_{ab} of not finding a and b coexisting on any of a set of n islands, which need not have the same species numbers, is given by the product

$$Z_{ab} = \prod_{i=1}^{i=n} [1 - J_a(S_i)J_b(S_i)] \qquad (5)$$

where the product is taken over all n islands. Evaluation of eq. 5 for the species *M. mackinlayi* and *M. nigrirostris*, substituting J values from Figure 25 corresponding to the S values for all islands for which $J_M \neq 0, J_N \neq 0$, yields a no-coexistence probability Z_{ab} of 0.74. That is, incidence functions alone predict the probability of not finding M and N together on any of these six islands, and we do not have statistical evidence for invoking a compatibility rule. By analogy with other similar cases, however (cf. following section, "Assembly of the gleaning flycatcher guild"), where statistical evidence for incompatibility does exist, and because of the close similarity of *Macropygia mackinlayi* and *M. nigrirostris,* my guess is that availability or surveys of more islands would show their coexistence to be incompatible and not just improbable. It should also be realized that incompatibility of these two species is an important *reason* for the form of their incidence functions: viz., that the supertramp *M. mackinlayi* is absent from large islands where occurrence of the A-tramp *M. nigrirostris* is likely, and vice versa for small islands. This is demonstrated by Figure 19, which shows that removal of *M. nigrirostris* and *M. amboinensis* from the species pool converts *M. mackinlayi* from a supertramp (in the Bismarcks) to a D-tramp (in the Solomons).

Combination rules.

The incidence functions of Figure 25 suggest that the combination *AMR* should occur frequently on islands with a medium species number. This combination does not violate the presumed compatibility rule forbidding *MN.* Neither does it violate incidence rules, since Figure 25 shows J_A, J_M, and J_R all to be high in an S range where J_N is zero or at least far below 1.0. The value of the product $J_AJ_MJ_R$ suggests that, if there were no restrictions on cuckoo-dove combinations other than those implicit in compatibility rules and incidence rules, the combination *AMR* should occur on about one-third of all islands supporting 43 to 55 species, and on a somewhat lower proportion of islands with 25–43 or 55–70 species. Nevertheless, there is no known island with the combination *AMR.* Since most islands of sufficient size or S potentially to support this combination have been ornithologically explored, it appears likely that *AMR* does not exist in nature.

The statistical test of this conclusion is similar to the one just considered for the compatibility of M and $N.$ Whether we should attach significance to the actual nonexistence of *AMR* depends on whether there are enough real islands with sufficiently high $J_AJ_MJ_R$ products in an appropriate range of the incidence functions. If there were only a small number of islands in the range of high J_A, J_M, and J_R and low J_N, it could easily arise by chance that *AMR* would be found on none of these islands despite its being a permissible combination. To evaluate this possibility, we define $P_{i,X}$ as the probability that a certain combination X will occur on a certain island i, where $P_{i,X}$ takes account only of incidence functions.[1] For an arbitrary guild consisting of species $a, b, c, d, e, \ldots, j-1, j$, the probability that the combination abc will occur on an island i of species number S_i is given by

$$P_{i,abc}(S_i) = [J_a(S_i)][J_b(S_i)][J_c(S_i)] \prod_{x=d}^{x=j} [1 - J_x(S_i)] \quad (6)$$

$[1 - P_{i,abc}(S_i)]$ is then the probability that the island will not support abc. The product

$$Y(X) = \prod_{i=1}^{i=n} [1 - P_{i,X}(S_i)] \qquad (7)$$

evaluated for the combination $X = AMR$ with the product taken over all n islands of the Bismarck Archipelago, then has the following meaning: $Y(AMR)$ is the combination probability that AMR would not be observed on any actual Bismarck island if there were no rules about combinations other than those implicit in incidence functions.[1]

The evaluation of $Y(AMR)$ is simplified by the fact that $P_{i,AMR}(S) = 0$, $[1 - P_{i,AMR}(S_i)] = 1$ for all islands with $S > 77$, since J_M then is zero, and for all islands with $S < 22$, since J_R then is zero. Table 8 lists J_A, J_M, J_N, and J_R values read off from Figure 25, and $P_{i,AMR}$ calculated from eq. 6, for all Bismarck islands that have $22 < S < 77$. As evaluated from the product of the $(1 - P_{i,AMR})$ terms in the last column of Table 8, $Y(AMR)$ is 0.027. That is, given the actual number of well-explored Bismarck islands and actual incidence functions, the probability of failing to find AMR on any island would be only 0.027 if all constraints were implicit in incidence functions. We conclude that there must be additional *combination rules* whose existence could not have been suspected from Figure 25, and one of which forbids the coexistence of *amboinensis*, *mackinlayi*, and *Reinwardtoena*. Note that the subcombinations *AM*, *MR*, and *AR* all occur on real islands, yet *AMR* is forbidden.

There are two further combinations whose existence is not forbidden by incidence rules or compatibility rules but which nevertheless do not exist on real Bismarck islands: *R* and *AN*. The *AN* combination is also absent from the New Guinea region, where *amboinensis* and *nigrirostris* are both present; and the *R* combination is also absent from the New Guinea region, Moluccas, and Solomons, where *Reinwardtoena* is present along with either one or two other species of cuckoo-doves. Thus, there may be additional combination rules forbidding *R* and *AN*. In these cases, however, there are not enough islands with appropriate incidence values to give us as much confidence as in the *AMR* case that the combination

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[1] Equations 6 and 7 take account of incidence functions but not of compatibility rules. For a more exact evaluation of $Y(X)$, the probabilities of combinations forbidden by compatibility rules must somehow be redistributed among compatible combinations. The forms of eqs. 4 and 6 differ, because eq. 4 calculates the probability that species a and b will coexist, either by themselves or as part of a larger combination, whereas eq. 6 calculates the probability that a, b, and c will coexist by themselves, not as part of a larger combination.

Table 8. Combination probability of the cuckoo-dove species AMR for 16 Bismarck Islands

S	J_A	J_M	J_R	J_N	$P_{i,AMR}$	$1 - P_{i,AMR}$
29	0.13	0.70	0.16	0	0.01	0.99
32	0.25	0.71	0.21	0	0.04	0.96
32	0.25	0.71	0.21	0	0.04	0.96
34	0.34	0.72	0.26	0	0.06	0.94
37	0.59	0.72	0.32	0	0.14	0.86
38	0.69	0.71	0.34	0	0.17	0.83
39	0.75	0.71	0.36	0	0.19	0.81
43	0.97	0.68	0.46	0	0.30	0.70
45	1.0	0.67	0.50	0	0.34	0.66
46	1.0	0.66	0.53	0	0.35	0.65
53	1.0	0.52	0.72	0.08	0.34	0.66
55	1.0	0.48	0.77	0.10	0.33	0.67
59	1.0	0.35	0.85	0.17	0.25	0.75
60	1.0	0.31	0.86	0.18	0.22	0.78
62	1.0	0.25	0.88	0.20	0.18	0.82
65	1.0	0.17	0.92	0.24	0.13	0.87

The cuckoo-dove combination *AMR* occurs on no known island. The table calculates whether this finding is expected by chance, given only the constraints of incidence functions. Only in the range $22 < S < 77$ are the incidences J_A, J_M, and J_R all nonzero. Column 1 gives the species number on all 16 Bismarck islands in this S range whose resident cuckoo-doves are known. Columns 2-5 are the incidences corresponding to the S of each island for each cuckoo-dove species, read from the incidence functions of Figure 25. Column 6 gives the probability $P_{i,AMR}$ [calculated from these incidences as $J_A J_M J_R(1 - J_N)$, eq. 6] that the combination *AMR* will occur on an island with this S; column 7 gives $1 - P_{i,AMR}$, the calculated probability that *AMR* will not occur on the island. The product $Y(AMR)$ of all the terms in the last column (eq. 7) is 0.027, the probability that *AMR* would occur on none of the 16 islands if the only constraints were those of incidence functions. Since this probability is very low but *AMR* in fact occurs on none of the 16 islands, the combination is presumed to be forbidden for some reason not implicit in incidence functions.

would have been observed if it were not explicitly forbidden.

Figure 27 plots the observed combination incidence $C_X(S)$ as a function of island species number S, for the six permitted cuckoo-dove combinations of the Bismarcks. For any $S = S_i$, the sum $\Sigma\, C_X(S_i)$, taken over all X, is 1.0. For any given S_i, there are generally only two or three combinations that have any significant probability of occurring. By considering separately the dependence of S on island area and isolation, we may eventually be able to predict with higher probability what combination a particular island will support.

Historical proof of resistance to invasion, or of feasibility of assembly.

The derivation of the assembly rules summarized in Table 7 was based entirely on observation of existing distributions. These rules imply that certain, but not all, combinations of cuckoo-doves form stable subcommunities that resist the invasion of other cuckoo-dove species. Invasion of such stable communities by a species

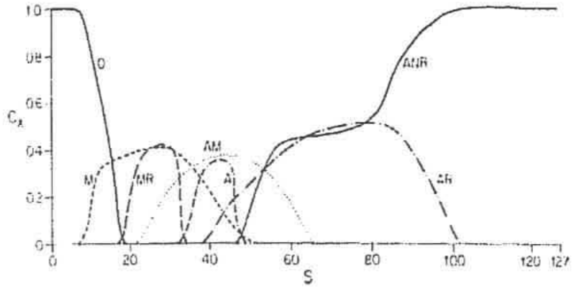


Figure 27 Ordinate, the observed combination incidence C_X for each of the six permitted cuckoo-dove combinations of the Bismarcks, as a function of the total number of bird species on an island (abscissa). This graph is constructed in the same way as the incidence functions of Figure 4–15, except that what is plotted is the incidence of the indicated combination, not the incidence of a species regardless of what combination it occurs in. Symbols for combinations have the same meaning as in Table 7, except that the additional symbol 0 means no resident species of cuckoo-dove.

whose addition would result in a forbidden combination is doomed to failure, unless the invader can eliminate one of the original members of the community. In five cases it has been possible to document directly, by historical evidence, that permitted combinations of species do resist forbidden invaders:

(a) *Reinwardtoena browni, M. nigrirostris,* and *M. amboinensis* have been the resident cuckoo-doves of New Britain throughout this century (combination *ANR*). There is no resident population of *M. mackinlayi,* whose addition would create a combination forbidden by compatibility rules (*AMNR*). However, vagrant individuals of *M. mackinlayi* have been encountered by O. Meyer and A. Eichhorn. Since *M. mackinlayi* is an abundant breeder on small islands within one mile of New Britain, it must be a frequent invader.

(b,c) *M. amboinensis* and *M. mackinlayi* are the resident cuckoo-doves of Vuatom. O. Meyer recorded repeated unsuccessful invasions of *Reinwardtoena browni,* which would have yielded *AMR* (forbidden by combination rules), and of *M. nigrirostris,* which would have yielded *AMN* (forbidden by compatibility rules).

(d) *Reinwardtoena reinwardtsi* and *Macropygia mackinlayi* have been resident on Karkar for at least the last 60 years. Several vagrants of *M. nigrirostris* were collected in 1969. *MNR* is forbidden by compatibility rules.

(e) *Macropygia amboinensis* and *Reinwardtoena browni* have coexisted on Umboi since at least 1913. There are four records of vagrants of *M. mackinlayi* (*AMR* forbidden by combination rules).

On the other hand, two successful invasions of cuckoo-dove subcommunities have been documented, both resulting in the permitted combination *AM. M. mackinlayi* was the sole species breeding on Long in 1933, but by 1972 *M. amboinensis* as well had become a widely distributed breeder, though it was still less common than its congener. On Vuatom, *M. amboinensis* was the sole breeding species in 1906, but *M. mackinlayi* had also become an abundant breeder by 1930.

In all five cases of unsuccessful invasions cited, populations of the forbidden species breed on islands within a short distance of the island from which they are excluded (*M. mackinlayi* 1 mile from New Britain, *Reinwardtoena browni* and *M. nigrirostris* 4 miles from Vuatom, *M. nigrirostris* 10 miles from Karkar, *M. mackinlayi* 10 miles from Umboi). Only for

Vuatom are records of a long-term resident observer available. However, the conclusion seems inescapable for the other cases as well that the documented invasions of forbidden species are not isolated occurrences.

We can now reconsider the problem of the "empty squares" on the *Macropygia* checkerboard (Figure 20). The dilemma was that most Bismarck islands are occupied by either *M. nigrirostris* or *M. mackinlayi* in checkerboard fashion. However, six islands support neither species, and there is no single additional species whose distribution would complete the checkerboard. Of these six islands, the four most species-rich ($S = 40–59$) prove to support both *M. amboinensis* and *Reinwardtoena.* Although *M. mackinlayi* can coexist separately with either of these two species, the combination *AMR* is forbidden, as shown by the analysis of Table 8 as well as by *M. mackinlayi's* unsuccessful invasion of Umboi's *AR* community. While the combination *ANR* is not forbidden, its probability of occurrence exceeds 0.5 only on islands with $S > 80$ (Figure 27), indicating that an established *AR* combination can frequently exclude *M. nigrirostris* on more species-poor islands. The two most species-poor islands ($S = 38, 39$) that correspond to empty squares prove to support *M. amboinensis.* The combination *AN* is forbidden by incidence rules (lower $S_{\text{crit}} = 45$ for *M. nigrirostris*). The combination *AM* is not forbidden, but its probability of occurrence is only 0.35 on islands with $S = 38$ or 39, indicating that an established *M. amboinensis* population can often exclude *M. mackinlayi* on islands with this *S.* Thus, the empty squares are actually filled by a species or a combination of species that make invasion difficult or impossible both for *M. nigrirostris* and for *M. mackinlayi.*

Assembly of the Gleaning Flycatcher Guild

Whereas some flycatchers sally to catch insects in mid-air, seven Bismarck species glean insects from leaves and branches: the B-tramp *Pachycephala pectoralis* (abbreviated *P*), supertramps *Pachycephala melanura dahli* (*D*) and *Monarcha cinerascens* (*C*), A-tramps *Monarcha verticalis* superspecies (*V*), *Monarcha chrysomela* (*R*), and *Myiagra hebetior* (*H*), and C-tramp *Myiagra alecto* (*A*). One or more of these flycatcher species is present on every Bismarck island larger than 10 acres, and on most smaller islets as well. No single island, however, supports all seven species. The smallest or most species-poor islands have only one or two species, whereas the richest islands have four or five species. Figure 28 gives incidence functions of all seven species.

Because the gleaning flycatcher guild contains more species and more possible combinations than does the cuckoo-dove guild, a complete analysis of assembly rules would require more islands than are available or have been explored in the Bismarcks. However, the available information does make certain regularities in assembly obvious.

Pachycephala pectoralis and *P. m. dahli* never coexist on an island, either by themselves or as part of a larger combina-

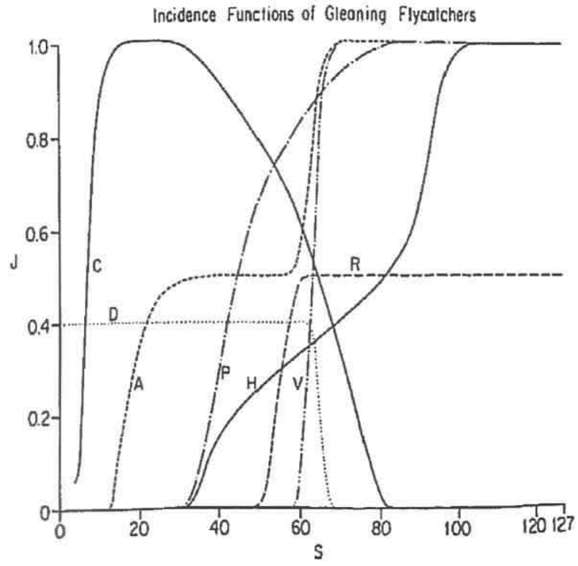


Figure 28 Incidence functions for the gleaning flycatchers *Monarcha cinerascens* (*C*), *Pachycephala melanura dahli* (*D*), *Myiagra alecto* (*A*), *Pachycephala pectoralis* (*P*), *Myiagra hebetior* (*H*), *Monarcha verticalis* (*V*), and *Monarcha chrysomela* (*R*) in the Bismarcks.

tion. These species are products of a recent speciation and are the two most similar gleaning-flycatchers, both ecologically and morphologically. J_P is 0 for $S < 32$, and J_D is 0 for $S > 69$, but there are 14 well-explored islands in the range $32 < S < 69$ in which coexistence is not prohibited by incidence functions. The no-coexistence probability Z_{PD} that *P* and *D* by chance would not be found together on any of these 14 islands is calculated from eqs. 4 and 5 in Table 9, as 0.036. That is, the failure of *P* and *D* to coexist is not expected from their incidence functions, and we must assume *P* and *D* to be incompatible, as we might have guessed on biological grounds.

Pachycephala m. dahli and *Monarcha chrysomela* also coexist on no island, either by themselves or as part of a larger combination. In this case there is less overlap of incidence functions than for *P. pectoralis* and *P. m. dahli:* only in the range $50 < S < 69$, where there are seven well-explored islands, are J_D and J_R both nonzero. Evaluation of the noncoexistence probability Z_{DR} from eq. 5 yields 0.37. That is, incompatibility is not established at a statistically significant level, and noncoexistence might perhaps have been ex-

Table 9. No-coexistence probability of the flycatcher species *P* and *D*

Species number	Observed incidences		Calculated probabilities	
S	J_P	J_D	$J_P J_D$	$1 - J_P J_D$
34	0.05	0.40	0.02	0.98
37	0.19	0.40	0.08	0.92
38	0.23	0.40	0.09	0.91
39	0.27	0.40	0.10	0.90
43	0.44	0.40	0.18	0.82
45	0.51	0.40	0.20	0.80
46	0.55	0.40	0.22	0.78
53	0.72	0.40	0.29	0.71
55	0.75	0.40	0.30	0.70
59	0.81	0.40	0.32	0.68
60	0.82	0.40	0.33	0.67
62	0.84	0.40	0.34	0.66
65	0.89	0.22	0.20	0.80
65	0.89	0.22	0.20	0.80

The flycatcher species *P* and *D* coexist on no known island. The table calculates whether this finding is expected by chance, given only the constraints of incidence functions. Only in the range $32 < S < 69$ are the incidences J_P and J_D both nonzero. Column 1 gives the species number of all 14 Bismarck islands in this *S* range whose resident flycatchers are known. Columns 2 and 3 are the incidences J_P and J_D corresponding to the *S* of each island, read from the incidence functions of Figure 28. Column 4 gives the probability (calculated from these incidences as $J_P J_D$) that species *P* and *D* will coexist on an island with this *S*; column 5 gives $p_{i,PD} = 1 - J_P J_D$ (eq. 4), the calculated probability that *P* and *D* will not coexist on the island. The product Z_{PD} of all the terms in the last column (eq. 5) is 0.036, the probability that *P* and *D* would coexist on none of the 14 islands if the only constraints were those of incidence functions. Since this probability is very low but *P* and *D* in fact coexist on none of the islands, their coexistence is presumed to be forbidden for some reason not implicit in incidence functions: i.e., they are presumed incompatible.

pected from incidence functions alone. *P. m. dahli* and *M. chrysomela* are sufficiently different (the latter smaller, moving more rapidly, avoiding dense vegetation) that incompatibility does not seem likely.

If an island has a single flycatcher species, that species is either species *C* (12 islands), *D* (8 islands), or rarely *A* (1 island). *H*, *P*, *R*, and *V* never occur alone.

If an island has two flycatcher species, only four combinations are permissible: *AC* (3 islands), *CD* (6 islands), *CP* (1 island), *AD* (1 island). As discussed above, the combination *DP* and conceivably the combination *DR* are incompatible, but all other forbidden two-species combinations occur as parts of larger combinations on islands with more flycatcher species.

If an island has three flycatcher species, the observed combinations are *APV* (3 islands), *CPR* (1 island), *ACP* (1 island), and *ACV* (1 island).

If an island has four flycatcher species, the observed combinations are (1 island each) *AHPV*, *CHPV*, *ACDV*, *ACDH*, *ACPR*, and *ACRV*. Note that the combination *CD* is favored over *AC* on two-flycatcher islands, while the reverse is true on four-flycatcher islands.

The only permissible five-species combination is *AHPRV* (3 islands).

In order to assess the extent to which these assembly rules are predictable from incidence functions alone, the simple case of the two-flycatcher islands was analysed approximately, as follows (Table 10). From the total species number S_i on each of the known two-flycatcher islands, $J(S_i)$ was read off of the incidence functions (Figure 28) for each species, the product $J_a J_b$ was calculated for each possible flycatcher pair *a* and *b* on each island, except for the incompatible pair *DP*, and the relative values of the products $J_a J_b$ for each pair summed over all islands were compared with the actual incidence of occurrence of each flycatcher pair. As shown in Table 10, this calculation predicts approximately the permitted two-flycatcher combinations and their relative frequency, except that the supertramp combination *CD* seems more frequent than expected. That is, these species may "fit together" particularly well, and this fit is even better than expected simply from their supertramp incidence functions. Observations on more real islands are desirable to be certain that this conclusion is statistically significant.

The favored combinations are resistant to invasion. Vagrants of the supertramp *Monarcha cinerascens* (*C*) have been recorded, but have apparently not established resident populations, on Umboi (resident combination *APV*), New Ireland (*AHPRV*), and Dyaul (*AHPRV*). Vagrants of the supertramp *Pachycephala melanura dahli* (*D*) have appeared on Tolokiwa (resident combination *CP*), Umboi (*APV*) and New Britain (*AHPV*). The regular occurrence of these supertramps on small islets close to larger islands from which they are absent suggests continuous bombardment of islands with supertramp-excluding combinations by supertramp vagrants.

Reconsideration of the "empty squares" of the *Pachycephala pectoralis–P. m. dahli* checkerboard (Figure 21) shows that each island without a *Pachycephala* species is

Table 10. Two-species combinations of gleaning flycatchers

S	Actual	J_A	J_C	J_D	J_P	J_H	J_R	J_V	$J_A J_C$	$J_A J_D$	$J_C J_D$	$J_C J_P$	$J_A J_P$	$J_H J_A$	$J_H J_C$	$J_H J_D$	$J_H J_P$	$J_R J_P$	$J_R J_C$	$J_R J_A$
10	*CD*	0	0.90	0.40	0	0	0	0	0	0	0.36	0	0	0	0	0	0	0	0	0
13	*CD*	0.08	0.98	0.40	0	0	0	0	0.08	0.03	0.39	0	0	0	0	0	0	0	0	0
17	*CD*	0.24	1.00	0.40	0	0	0	0	0.24	0.10	0.40	0	0	0	0	0	0	0	0	0
18	*AC*	0.28	1.00	0.40	0	0	0	0	0.28	0.11	0.40	0	0	0	0	0	0	0	0	0
32	*CD*	0.50	1.00	0.40	0	0	0	0	0.50	0.20	0.40	0	0	0	0	0	0	0	0	0
34	*CD*	0.50	0.97	0.40	0.06	0.03	0	0	0.49	0.20	0.39	0.06	0.03	0.02	0.03	0.01	0	0	0	0
37	*AC*	0.50	0.95	0.40	0.19	0.10	0	0	0.48	0.20	0.38	0.18	0.10	0.05	0.10	0.04	0.02	0	0	0
39	*AC*	0.50	0.93	0.40	0.28	0.14	0	0	0.47	0.20	0.37	0.26	0.14	0.07	0.13	0.06	0.04	0	0	0
45	*CP*	0.50	0.86	0.40	0.51	0.21	0	0	0.43	0.20	0.34	0.44	0.26	0.12	0.18	0.08	0.11	0	0	0
53	*CD*	0.50	0.75	0.40	0.72	0.28	0.14	0	0.38	0.20	0.30	0.54	0.36	0.14	0.21	0.11	0.20	0.10	0.11	0.07
62	*AD*	0.69	0.58	0.40	0.85	0.35	0.50	0.37	0.40	0.28	0.23	0.49	0.59	0.24	0.20	0.14	0.30	0.43	0.29	0.35
$\Sigma J_X J_Y$, all islands									3.75	1.72	3.96	1.97	1.45	0.64	0.85	0.44	0.67	0.53	0.40	0.42
Number of islands, predicted									2.2	1.0	2.3	1.2	0.9	0.4	0.5	0.3	0.4	0.3	0.2	0.2
Number of islands, actual									3	1	6	1	0	0	0	0	0	0	0	0

This table attempts to predict the relative frequency of each two-species combination of gleaning flycatchers on Bismarck islands, from the incidence functions of Figure 28. The first column lists the total species number on each Bismarck island supporting two (and only two) flycatcher species; the second column gives the actual two-species combination on each island. Columns 3–9 give J values for each species corresponding to the S of each island, read off from Figure 28. Columns 10–21 give the pair products of these J values, omitting the incompatible pair *PD* (cf. Table 9) and all pairs for which the sum of the product $J_X J_Y$ (summed over all 11 islands) is less than 0.4 (i.e., *DR*, *HR*, and all pairs that include species *V*). This sum of the products $J_X J_Y$ is given for all remaining pairs in row 12. The sum of these $J_X J_Y$ sums for all pairs except the incompatible pair *PD* is 18.53. Row 13 gives for each pair listed in the table the value of $(\Sigma J_X J_Y)(11/18.53)$, the predicted number of islands on which the pair should occur if the only constraints were those of incidence functions plus incompatibility of *PD*. The last row gives the actual number of islands of occurrence. The actual numbers and predicted numbers agree fairly well, except that *CD* apparently occurs more often than expected.

occupied by one or more other species of the gleaning flycatcher guild. One "empty" island supports the combination *ACV*, 5 support *AC*, and 13 support *C* alone. Each of these combinations can coexist with one or either of the *Pachycephala* species on a larger (more species-rich) island but can exclude *Pachycephala* on a smaller (more species-poor) island.

Assembly of the Myzomelid-Sunbird Guild

In the New Guinea region two superficially similar groups of birds serve as ecological counterparts of the New World's hummingbirds (cf. Karr and James, Chapter 11, Figure 1): sunbirds (family Nectariniidae), represented in the Bismarcks by the D-tramp *Nectarinia jugularis* and the C-tramp *Nectarina sericea* (abbreviated *J* and *S*, respectively), and honeyeaters (family Meliphagidae) of genus *Myzomela*, represented in the Bismarcks by the supertramps *M. sclateri* (*L*) and *M. pammelaena* (*P*), the A-tramp *M. cruentata* (*C*), and the high-*S* species *M. cineracea* (*X*), *M. pulchella* (*Y*), and *M. erythromelas* (*Z*). Each of the latter three species is present only on one or two of the largest islands, but the other species are more widespread. Figure 29 presents incidence functions. All known Bismarck islands except one tiny islet and the small, recently defaunated volcano Ritter support at least one member of this guild. *M. cineracea* and *M. pammelaena* are larger than the other myzomelids, which are similar in size to the two sunbirds. In the Bismarcks, as elsewhere, the small myzomelids all maintain average spatial segregation. Low islands have only one small myzomelid, whereas the two highest Bismarck islands have two species segregating by altitude. The two sunbirds overlap spatially with each other but tend to segregate spatially from the similar-sized small myzomelids (cf. Figure 41). Large myzomelids such as *X* and *P* overlap spatially with small myzomelids or sunbirds. For instance, *X* and *S*, *X* and *Z*, *X* and *C*, *P* and *J*, and *P* and *L* overlap spatially in the Bismarcks. All eight species are similar in taking nectar and insects from flowers, and in gleaning insects off leaves and twigs. The guild is of interest in consisting of two distinct families whose species are nevertheless exceptionally similar in ecology and exhibit obvious interfamilial aggressive behavior (Ripley,

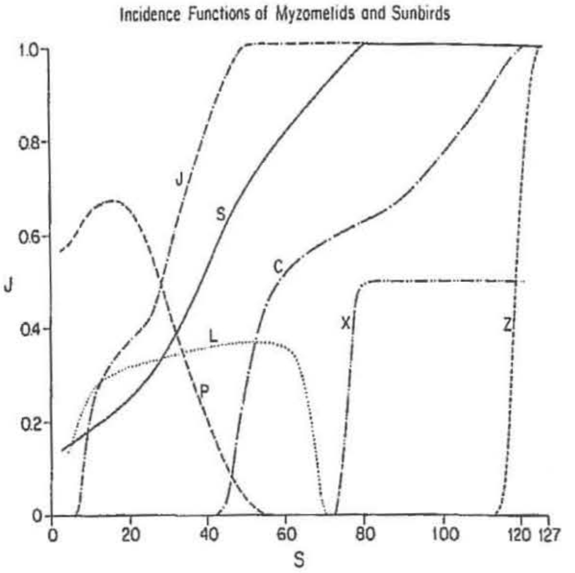


Figure 29 Incidence functions for the myzomelid-sunbird guild in the Bismarcks: *Myzomela pammelaena* (*P*), *M. sclateri* (*L*), *M. cineracea* (*X*), *M. erythromelas* (*Z*), *M. cruentata* (*C*), *Nectarinia jugularis* (*J*), and *N. sericea* (*S*). The remaining species, *M. pulchella*, is confined to an island with $S = 101$.

Table 11. Two-species combinations of myzomelids and sunbirds

S	Actual	J_P	J_L	J_J	J_S	J_C	$J_L J_P$	$J_J J_P$	$J_P J_S$	$J_J J_L$	$J_L J_S$	$J_J J_S$	$J_C J_L$	$J_C J_J$	$J_C J_S$	$J_C J_P$
9	*LS*	0.63	0.24	0.15	0.18	0	0.15	0.09	0.11	0.04	0.04	0.03	0	0	0	0
9	*LS*	0.63	0.24	0.15	0.18	0	0.15	0.09	0.11	0.04	0.04	0.03	0	0	0	0
15	*JP*	0.67	0.30	0.32	0.22	0	0.20	0.21	0.15	0.09	0.07	0.07	0	0	0	0
16	*JP*	0.68	0.30	0.33	0.22	0	0.20	0.22	0.15	0.10	0.07	0.07	0	0	0	0
17	*JP*	0.68	0.30	0.34	0.23	0	0.20	0.23	0.16	0.10	0.07	0.08	0	0	0	0
32	*JP*	0.40	0.35	0.61	0.36	0	0.14	0.24	0.14	0.21	0.13	0.22	0	0	0	0
37	*JS*	0.27	0.35	0.74	0.44	0	0.09	0.20	0.12	0.26	0.15	0.33	0	0	0	0
38	*JS*	0.24	0.35	0.76	0.46	0	0.08	0.18	0.11	0.27	0.16	0.35	0	0	0	0
43	*JP*	0.14	0.36	0.88	0.58	0	0.05	0.12	0.08	0.32	0.21	0.51	0	0	0	0
45	*PL*	0.11	0.36	0.92	0.61	0.02	0.04	0.10	0.07	0.33	0.22	0.56	0.01	0.02	0.01	0
55	*JS*	0	0.37	1.00	0.75	0.44	0	0	0	0.37	0.28	0.75	0.16	0.44	0.33	0
59	*JS*	0	0.36	1.00	0.80	0.50	0	0	0	0.36	0.29	0.80	0.18	0.50	0.40	0
$\Sigma J_X J_Y$, all islands							1.30	1.68	1.20	2.49	1.73	3.80	0.35	0.96	0.74	0
Number of islands, predicted							1.1	1.4	1.0	2.1	1.5	3.2	0.3	0.8	0.6	0
Number of islands, actual							1	5	0	0	2	4	0	0	0	0

This table attempts to predict the relative frequency of each two-species combination of myzomelids and sunbirds on Bismarck islands in the same manner as Table 10, from the incidence functions of Figure 29. The first column lists the total species number on each Bismarck island supporting two (and only two) myzomelid-sunbird species; the second column gives the actual two-species combination on each island. Columns 3–7 give J values for each species corresponding to the S of each island, read off from Figure 29 and omitting species X, Y, and Z, for which J is 0 throughout the range $9 \leq S \leq 59$. Columns 8–16 give the pair products of these J values, and row 13 gives the sum of the product $J_X J_Y$ (summed over all 12 islands) for each pair. The sum of all these $J_X J_Y$ sums for all pairs is 14.25. Row 14 gives for each pair the value of $(\Sigma J_X J_Y)(12/14.25)$, the predicted number of islands on which the pair should occur if the only constraints were those of incidence functions. The last row gives the actual number of islands of occurrence. The actual numbers and predicted numbers agree fairly well, except that *JP* occurs more often, and *PS* and *JL* less often, than expected.

1959) and competitive effects on distributions (Diamond, 1970a).

As with the gleaning flycatcher guild, the number of species in the myzomelid-sunbird guild precludes a complete analysis of assembly rules based on the available number of real islands. However, some regularities in assembly are obvious:

If a Bismarck island contains a single guild member, it is either *P* (14 islands), *L* (5 islands), *S* (3 islands), or *J* (2 islands), never *C, X, Y,* or *Z.*

If an island contains two members, the permissible combinations are *JP* (5 islands), *JS* (4 islands), *LS* (3 islands), or *LP* (1 island). The four permuted species are the same ones as are permitted on one-species islands. However, two of the six possible pairs drawn from these four species, *PS* and *JL,* never occur on two-species islands, although *J* and *L* do coexist on three-species islands. The species *C, X, Y,* and *Z* are absent from two-species islands as well as from one-species islands.

On three-species islands the permissible combinations are *JSL* (3 islands), *JSX* (1 island), *JSC* (3 islands), and *JPL* (2 islands). Only 2 islands have higher combinations (*JSCY* and *JSCXZ,* each on 1 island). In the Bismarcks as elsewhere, the combination *JS* appears as part of most three-species combinations and all four- and five-species combinations.

Table 11 attempts to predict the permitted two-species combinations and their relative frequencies on the basis of incidence functions alone. The calculation is carried out in the same manner as for the gleaning flycatchers in Table 10. It appears that the incidence functions fail to predict the nonoccurrence of the combinations *PS* and *JL,* or the high frequency of *JP.* These combinations must have special difficulties or special advantages of fit. Frequencies of other combinations are approximately as predicted from incidence functions.

Reexamination of the numerous empty squares in the checkerboard formed by the distributions of the four small myzomelids *C, L, Y,* and *Z* shows that 29 of the 31 empty squares are occupied by another guild member (*J, P,* or *S*), or else by a pair or trio of guild members (*JP, JS,* or *JSX*).

Assembly of the Fruit-Pigeon Guild

On New Guinea live 18 species of fruit pigeons, 12 smaller species in genus *Ptilinopus* and 6 larger species in genus *Ducula.* All are ecologically similar in being arboreal, living in the crowns rather than in the middle story, being exclusively frugivorous, not taking stones into the gizzard, and hence restricted to eating soft fruits that can be crushed by the gizzard wall. At a single locality in New Guinea lowland rainforest one encounters no more than 8 species, which form a graded size series, each species weighing approximately 1.5 times the next smaller species (average weights 49, 76, 123, 163, 245, 414, 592, and 802 g: see Figure 30). Size differences permit resource partitioning in two ways. First, larger pigeons can eat larger fruits, and may not find it energetically worthwhile to harvest smaller fruits (Figure 31; see also Hespenheide, Chapter 7). Second, smaller pigeons can perch on

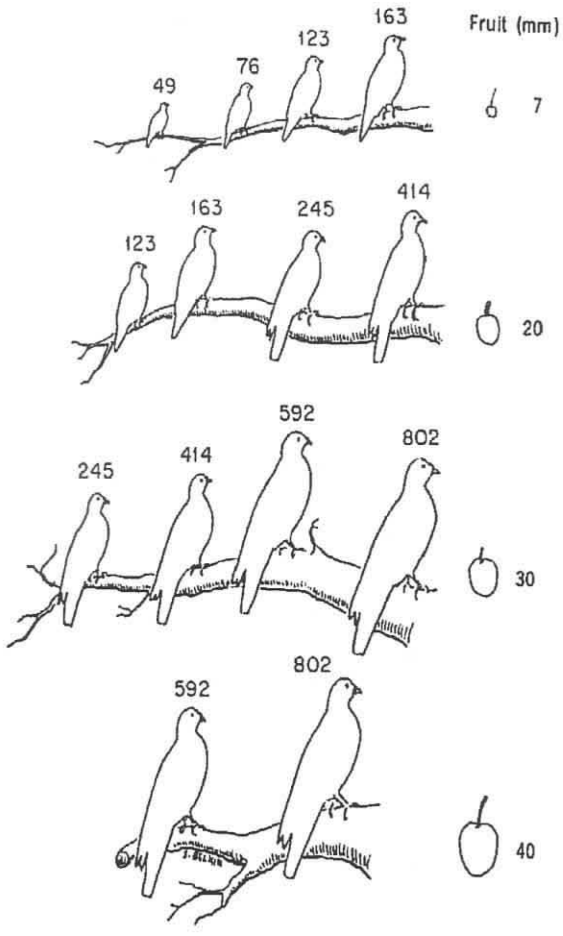


Figure 30 Schematic representation of niche relations among the eight species of *Ptilinopus* and *Ducula* fruit pigeons in New Guinea lowland rain forest. On the right is a fruit of a certain diameter (in millimeters), and on the left are pigeons of different weights (in grams) arranged along a branch. Each pigeon weighs approximately 1.5 times the next pigeon. Each fruit tree attracts up to four consecutive members of this size-sequence. Trees with increasingly large fruits attract increasingly large pigeons. In a given tree the smaller pigeons are preferentially distributed on the smaller, more peripheral branches. The pigeons having the weights indicated are: 49 g, *Ptilinopus nanus;* 76 g, *P. pulchellus;* 123 g, *P. superbus;* 163 g, *P. ornatus;* 245 g, *P. perlatus;* 414 g. *Ducula rufigaster;* 592 g, *D. zoeae;* 802 g, *D. pinon* (from Diamond, Copyright 1973 by the American Association for the Advancement of Science.)

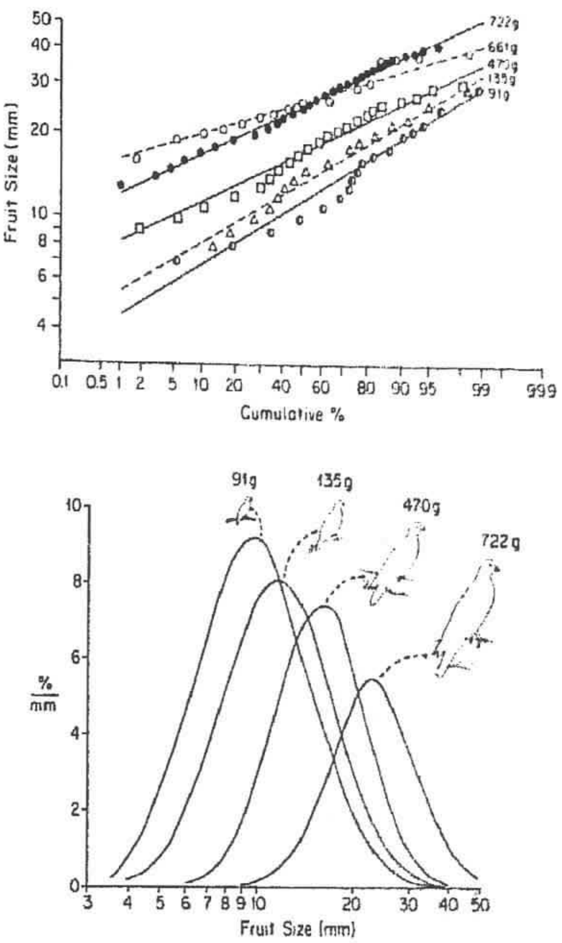


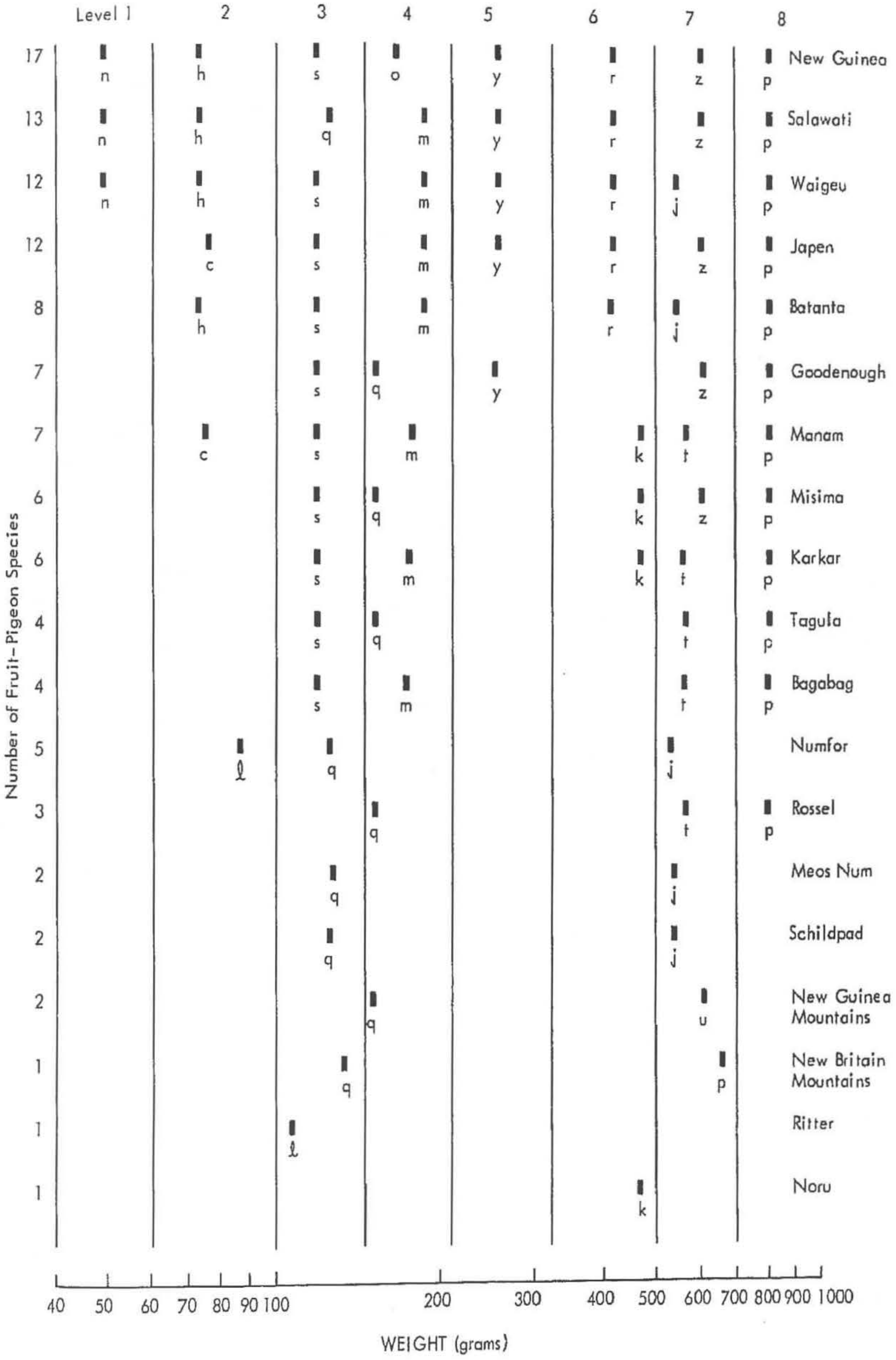
Figure 31 Proportions of fruit of different sizes eaten by fruit-pigeon species of different sizes. Above: cumulative proportion plotted on probability paper (cf. Cody, Chapter 10, Figure 7). Diameters of fruits in the stomachs of *Ducula rubricera* (symbols ●, body weight 722 g), *D. melanochroa* (○, 661 g), *D. pistrinaria* (□, 470 g), *Ptilinopus rivoli* (△, 135 g), and *P. solomonensis* (○, 91 g) were measured. The abscissa is the "cumulative" number of fruits up to a given diameter (ordinate, logarithmic scale), expressed as percentage of total number of fruits. Of the fruits measured as having a particular diameter, half were considered to have been accumulated in the interval preceding that diameter and half in the subsequent interval. The abscissa scale is such that if fruit sizes followed a log-normal distribution, the experimental points would define straight lines. This is approximately but not perfectly true; the deviations may be due to only a limited number of tree species in the size range suitable for each pigeon species being in fruit at the sampling time. All data were obtained in June–August 1972 on the Vitiaz-Dampier Islands. In the figure below, the straight lines fitted through the experimental points of the upper figure have been replotted as conventional log-normal curves (abscissa, log fruit size; ordinate, frequency distribution of sizes, expressed as percentage of all fruit lying within a size span of 1-mm width around the size value of the abscissa). Because the abscissa is logarithmic but the width-span linear, the areas under the curves of pigeons eating larger fruits are smaller. Note that larger pigeons eat larger fruits.

thinner twigs that would not support the weight of a heavier bird, and they can thereby reach some fruits inaccesible to a heavy bird. The remaining species besides the eight lowland rainforest birds are ten habitat vicariants that replace these rainforest species at higher altitudes, in savanna, in dry forest, or coastal forest. For instance, *Ptilinopus pulchellus* (76 g) in high-rainfall areas is replaced by *P. coronulatus* (75 g) in lower-rainfall areas; *P. superbus* (123 g) in forest is replaced by *P. iozonus* (112 g) in open country; and *Ducula zoeae* (592 g) at low elevations is replaced by *D. chalconota* (613 g) at high elevations. The eight New Guinea lowland rainforest species and their habitat vicariants can be considered as filling eight size levels, all of which except levels 1 (~49 g) and 5 (~245 g), corresponding to the smallest and largest species of genus *Ptilinopus,* are degenerate, i.e., occupied by several species. On a satellite island colonized by a vicariant but not by the corresponding lowland rainforest species, the vicariant generally expands into lowland rainforest. Assembly of fruit-pigeon guilds in lowland rainforest of satellite islands exhibits regular patterns with respect to the sequence in which levels are emptied as the guild becomes impoverished (Figure 32). (Figures 30, 31, and 32 resemble Figures 5, 7, and 4, respectively, in Chapter 13 by Brown, demonstrating similar size levels and vicariant species in desert rodent communities.) The fact that a given level may be occupied by any one of up to six species makes these regularities of community structure all the more striking, in their independence of species composition:

Five islands, exemplified by Salawati, Waigeu, and Japen in Figure 32, support 10–13 guild species. On two of these five islands (Salawati and Waigeu) all 8 levels are full, on two islands (e.g., Japen) level 1 (~49 g) is empty, and on one island level 5 (~245 g) is empty. Only level 8 (~800 g) is filled by the same species on all five islands and on New Guinea. For example, level 2 (~75 g) is occupied by *P. pulchellus* on three islands and on New Guinea, but by *P. coronulatus* on the remaining two islands.

Four islands, exemplified by Batanta, Manam, and Goodenough in Figure 32, support seven or eight guild species. Each island has either 5 or 6 levels occupied. Level 1 (~49 g) is empty on all four islands, and is also empty on all islands with

Figure 32 This figure shows how size levels of the fruit-pigeon guild are filled on islands with progressively poorer faunas. For each island named on the right, the rainforest fruit-pigeon species or habitat vicariant at each of eight size levels is indicated by a mark whose abscissa position indicates the bird's average weight (abscissa in grams, logarithmic scale), together with a letter abbreviation identifying the species. The numbers at the left are the number of fruit-pigeon species on each island. Most weights are average weights for the range of the species, but if geographical variation in size is well established, the weight for the local population is given (notice geographical variation in species *q, m,* and *p*). Abbreviations: *p* = *Ducula pinon,* *u* = *D. chalconota,* *z* = *D. zoeae,* *t* = *D. spilorrhoa,* *j* = *D. myristicivora,* *k* = *D. pistrinaria,* *r* = *D. rufigaster,* *y* = *Ptilinopus perlatus,* *m* = *Megaloprepia* (= *Ptilinopus*) *magnifica,* *o* = *P. ornatus,* *q* = *P. rivoli,* *s* = *P. superbus,* *l* = *P. solomonensis,* *c* = *P. coronulatus,* *h* = *P. pulchellus,* *n* = *P. nanus.* Notice that on progressively more impoverished islands (i.e., going from top to bottom in the figure) the first level to empty is level 1, followed by levels 2 and 5, followed by level 8.


Level 1
2
3
4
5
6
7
8
17 n h s o y r z p New Guinea
13 n h q m y r z p Salawati
12 n h s m y r j p Waigeu
12 c s m y r z p Japen
8 h s m r j p Batanta
7 s q y z p Goodenough
7 c s m k t p Manam
6 s q k z p Misima
6 s m k t p Karkar
4 s q t p Tagula
4 s m t p Bagabag
5 ℓ q j Numfor
3 q t p Rossel
2 q j Meos Num
2 q j Schildpad
2 q u New Guinea Mountains
1 q p New Britain Mountains
1 ℓ Ritter
1 k Noru
Number of Fruit-Pigeon Species
40
50
60
70
80
90
100
200
300
400
500
600
700
800
900
1000
WEIGHT (grams)

fewer than seven guild species. Both level 2 (~75 g) and level 5 (~245 g) are empty on two islands, and levels 3 (~123 g), 4 (~163 g), 7 (~592 g), and 8 (~802 g) are occupied on all four islands. For instance, level 7 (~592 g) is occupied by *Ducula myristicivora* (~535 g) on Batanta, by *D. spilorrhoa* (~563 g) on Manam, and by *D. zoeae* (~592 g) on Goodenough and Fergusson.

Seven islands, exemplified by Misima, Karkar, Tagula, Bagabag, and Numfor in Figure 32, support four to six guild species. Again, level 1 (~49 g) is empty on all islands. Level 5 (~245 g) is also empty on all islands, and levels 2 (~75 g) and 6 (~414 g) on most. Levels 7 or 8 or both, and 3 or 2 or both (usually just 3), are occupied on all islands.

Six islands, exemplified by Rossel and Meos Num in Figure 32, support three guild species. Levels 1, 2, and 5 are empty on all islands, and levels 4 and 8 are empty on all but one. Each island has one *Ptilinopus* species in level 3 (usually) or 4 (one island), and one *Ducula* species in level 7 (usually) or 8 (one island). The remaining species is always either another *Ptilinopus* vicariant in level 3 or another *Ducula* vicariant in level 7.

Four islands, exemplified by Schildpad in Figure 32, support two guild species. Three further "habitat islands" supporting two guild species are the mountains of New Guinea, the mountains of New Britain, and the mountains of New Ireland. One species is always a *Ptilinopus* in level 3 (usually) or level 4 (once), and the other is always a *Ducula* in level 6 or 7.

Eleven islands, exemplified by Ritter and Noru in Figure 32, support one guild species. This is always either a *Ptilinopus* in level 3 or a *Ducula* in level 6.

Thus, as the guild is progressively simplified on smaller or more remote islands, the first level to become empty is level 1, followed by levels 2 and 5, followed by level 8. These can be considered levels for high-*S* species only. Not only are these particular levels precarious, they are also the levels that on New Guinea either lack a habitat vicariant (levels 1 and 5) or have just one vicariant (levels 2 and 8). The precarious levels are the largest or smallest species of each genus, while the simplified communities generally consist of medium-size *Ptilinopus* and *Ducula*.

Of particular interest is a comparison of fruit-pigeon guilds on incompletely equilibrated islands with guilds on fully equilibrated islands. As discussed in the section "Background: the New Guinea biogeographic scene," species numbers on large islands that were connected to New Guinea by land bridges until the end of the Pleistocene are still far above equilibrium values expected from the species/area relation. For example, the land-bridge islands Japen and Waigeu each has about the same area as the oceanic island Biak, but each of the former has about twice as many total species, and three times as many species of fruit pigeons, as Biak. Some "contracted" islands that lacked land bridges to New Guinea but whose late-Pleistocene areas were much larger than their present areas are also still "supersaturated" in species number. Yet guild composition on these supersaturated islands is very similar to that on larger islands whose species number is at equilibrium. For instance, the same levels are occupied on the supersaturated land-bridge island Batanta as on the equilibrated island Manam (levels 2, 3, 4, 6, 7, 8); the supersaturated land-bridge islands Salawati and Waigeu have all 8 levels occupied, as on New Guinea, which is several hundred times larger; and the level occupancy on the supersaturated contracted islands Goodenough and Fergusson (levels 3, 4, 5, 7, 8) is nearly the same as that on the equilibrated islands Misima and Karkar (levels 3, 4, 6, 7, and 8). Misima actually shares five of its six species in common with Goodenough. Similarly, the exploded volcanoes Long and Ritter, which are still "underfilled" as to species number, have the same sets of fruit-pigeon species as those on islands one-tenth and one-hundredth, respectively, of their area.

Thus, a community not at equilibrium with respect to species number is similar, in the structure of its fruit-pigeon guilds, to an equilibrium community on a larger or smaller island. This implies that the time required for an island's species to become coadjusted to each other, and to sort into stable combinations by expulsion of excess species or by incorporation of suitable invaders, is much shorter than the relaxation time for equilibration of species number on the island. As a fauna relaxes towards equilibrium species number, community structure traverses a series of internally coadjusted states. Consideration of transition probabilities among permitted combinations suggests that relaxation may sometimes occur in steps (see section "Transition probabilities" for further discussion).

Finally, the fruit-pigeon guild is of interest in illustrating how an established species that could resist a single invader may be eliminated by two simultaneous invasions. Three *Ptilinopus* species are widespread in the lowlands of Bismarck islands: *P. superbus, P. insolitus,* and *P. solomonensis.* Each of the three possible two-species combinations (*superbus-insolitus, superbus-solomonensis, insolitus-solomonensis*) occurs on at least five islands, but there is no well-established instance of stable coexistence of all three species. The *solomonensis-insolitus* combination has successfully resisted *superbus* invaders on Vuatom and possibly on Tolokiwa, and the *superbus-insolitus* combination has successfully resisted *solomonensis* invaders on New Britain. In 1913 *P. solomonensis* was the sole *Ptilinopus* in the lowlands of Umboi, and was apparently abundant. Since Umboi is a large and species-rich island that could easily support two *Ptilinopus* species, an invasion either by *P. insolitus* or by *P. superbus* might have been predicted to have excellent prospects of success leading to coexistence with *P. solomonensis.* In fact, some time between 1913 and 1933 *both* of these two other species invaded, and by 1933 had become established though still uncommon. By 1972 both *P. insolitus* and *P. superbus* had become widespread, and *P. solomonensis* had contracted into a small area and narrow altitudinal range, where its chances of survival seem precarious. MacArthur (1972, pp. 43–45) has pointed out theoretical reasons why a species sandwiched between two close competitors is in a much more precarious situation than if it coexisted with just one competitor.

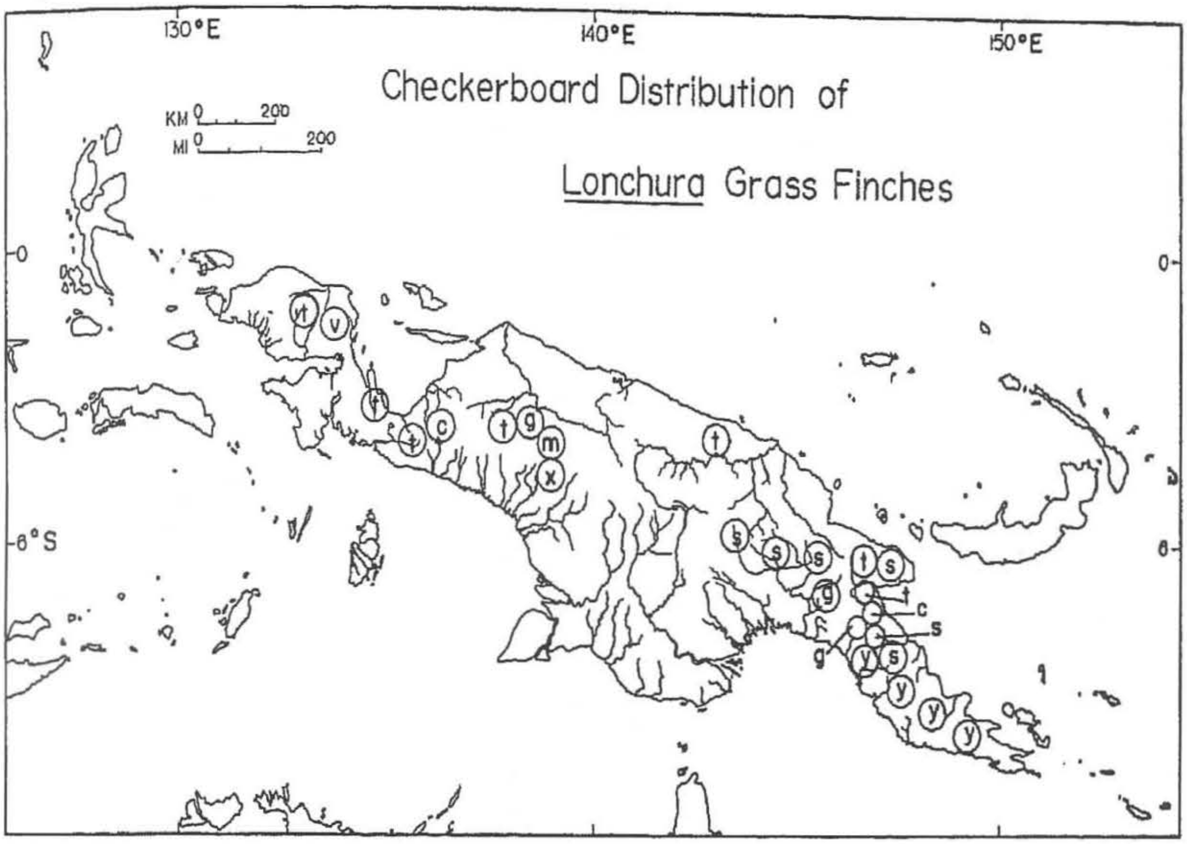
Replicate Communities on the Same Island

So far, we have been comparing the species composition of communities in physically similar environments on different islands. Let us now compare communities in physically similar environments at different localities within the same island.

Figure 33 presents a simple example. Natural grassland in New Guinea is largely confined to lowland marsh and savanna areas, mountaintops above timberline (ca. 11,000 feet), and landslide areas and strips along lakes and streams. Within the last few millenia human agriculture at 3000–8000 feet has created midmontane grassland "islands," which have been colonized by eight different species of grass finch of genus *Lonchura* (Diamond, 1972a, pp. 409–410). Four of these species are widespread in the lowlands, one is confined to the lowlands of southeast New Guinea, one is widespread in alpine grassland, and two are localized species of a midmontane lake or river system; three other localized lowland species failed to colonize midmontane grassland. In any given area a single finch species is ubiquitous in midmontane grassland over a considerable range of grass types and heights, altitudes, and rainfall conditions. However, the identity of the locally successful colonist varies in a geographically irregular checkerboard (Figure 33). This distribution pattern is very similar to the simple island checkerboards of Figures 20–24.

Figure 34 is a more complex checkerboard. Three similar honeyeaters of genus *Melidectes* (*M. ochromelas*, *M. belfordi*, and the *M. rufocrissalis* superspecies) live in midmontane forest. When considered individually, each has a peculiarly disjunct range and is absent from several portions of the New Guinea cordillera. Each species can coexist with each other species, so that the individual ranges do not form a checkerboard. When the ranges of the three species are considered together, however, it is clear that (a) each mountainous area supports two species that exclude the third; (b) the identity of the locally successful combination varies in irregular checkerboard fashion; and (c) each of the three possible combinations occurs in several areas (Diamond, 1972a, pp. 387–389). Among the three alpine species of *Melidectes* there is a similar checkerboard also involving all three possible two-species combinations, and there is evidence from one area that the locally missing third species has unsuccessfully invaded and is excluded. This pattern is similar to the two-species island checkerboard of lowland *Ptilinopus* pigeons in the Bismarcks (see discussion of *Ptilinopus superbus*, *P. insolitus*, and *P. solomonensis* in the section just preceding).

Figures 33 and 34 present in effect the ranges of patchily distributed species whose closest competitors are few in number and easy to guess biologically, and whose distributions combined with the distributions of the competing species form neat single-species (Figure 33) or two-species (Figure 34) checkerboards. Many more species are patchily distributed without any neat pattern involving competitors being apparent (Figures 35–38). For example, the tree creeper



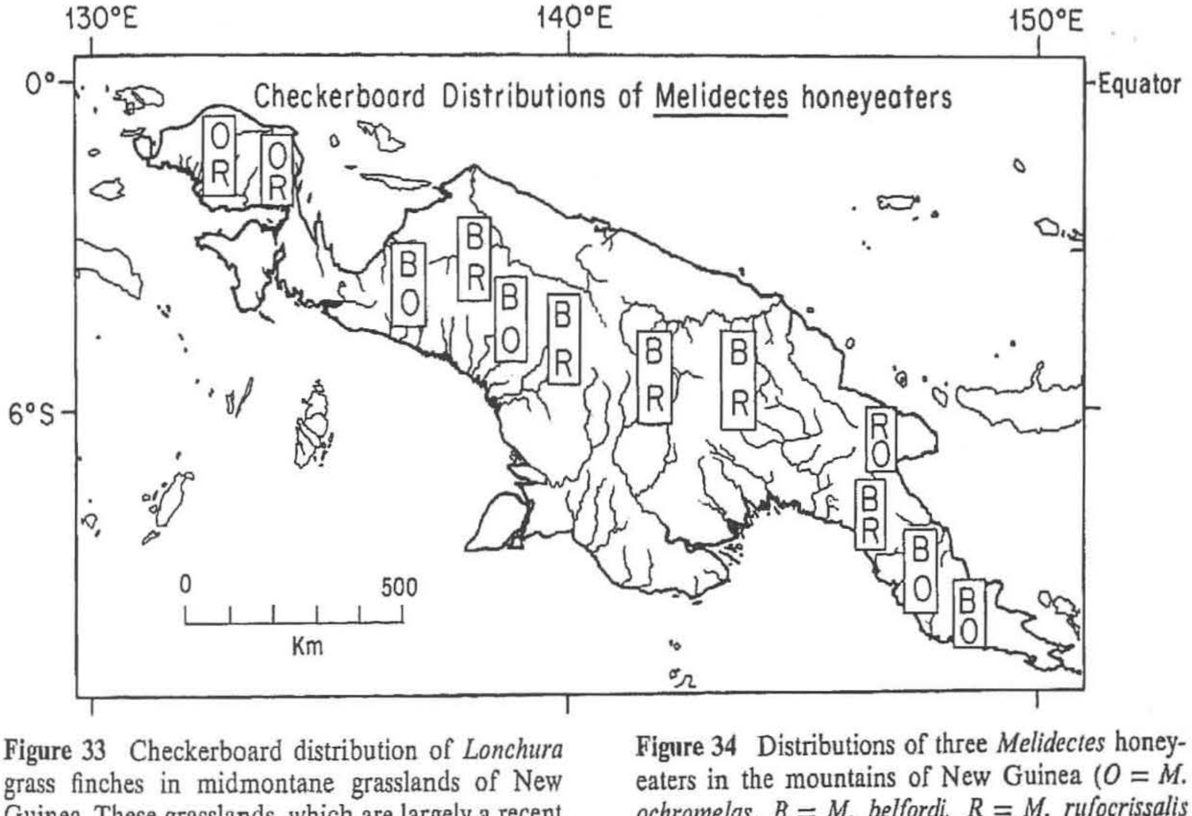


Figure 33 Checkerboard distribution of *Lonchura* grass finches in midmontane grasslands of New Guinea. These grasslands, which are largely a recent by-product of human agriculture, have been colonized by eight finch species of lowland grassland, alpine grassland, or midmontane lake or river systems. Most localities support only one species, but the identity of the locally successful colonist shows irregular geographical variation. *c* = *Lonchura castaneothorax*, *g* = *L. grandis*, *m* = *L. montana*, *s* = *L. spectabilis*, *t* = *L. tristissima*, *v* = *L. vana*, *x* = *L. teerinki*, *y* = *L. caniceps*.

Figure 34 Distributions of three *Melidectes* honeyeaters in the mountains of New Guinea (*O* = *M. ochromelas*, *B* = *M. belfordi*, *R* = *M. rufocrissalis* superspecies). Most mountainous areas of New Guinea support two species with mutually exclusive altitudinal ranges. At each locality depicted on the map, the letters above and below indicate the species present at higher and lower altitudes, respectively. All three possible two-species combinations occur in several disjunct areas, and the identity of the locally successful combination varies in irregular checkerboard fashion. (After Diamond, 1973.)

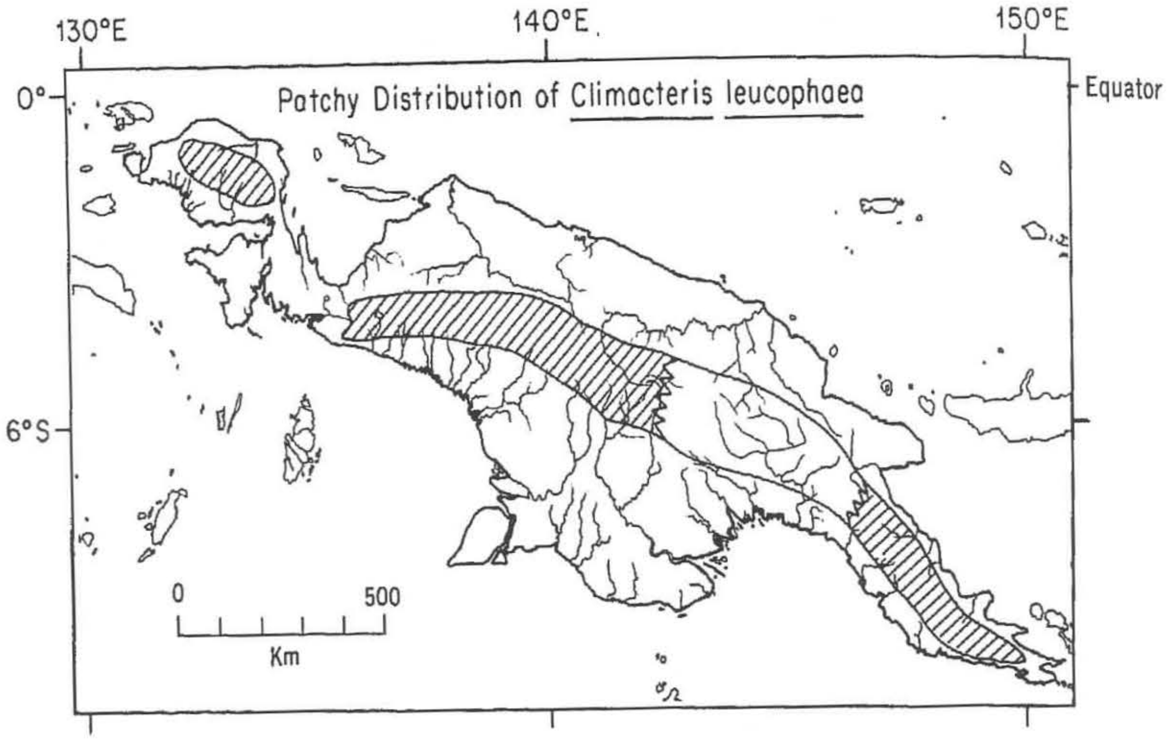


Figure 35 Patchy distribution of the tree creeper *Climacteris leucophaea* in the mountains of New Guinea. Although mountains and forest with similar tree bark extend uninterrupted for 1000 miles, and although there is no other New Guinea bird in the same family, this bark-feeding species has a distributional gap (unshaded area) of 250 miles in the middle of its range (hatched area). (From Diamond, 1972a.)

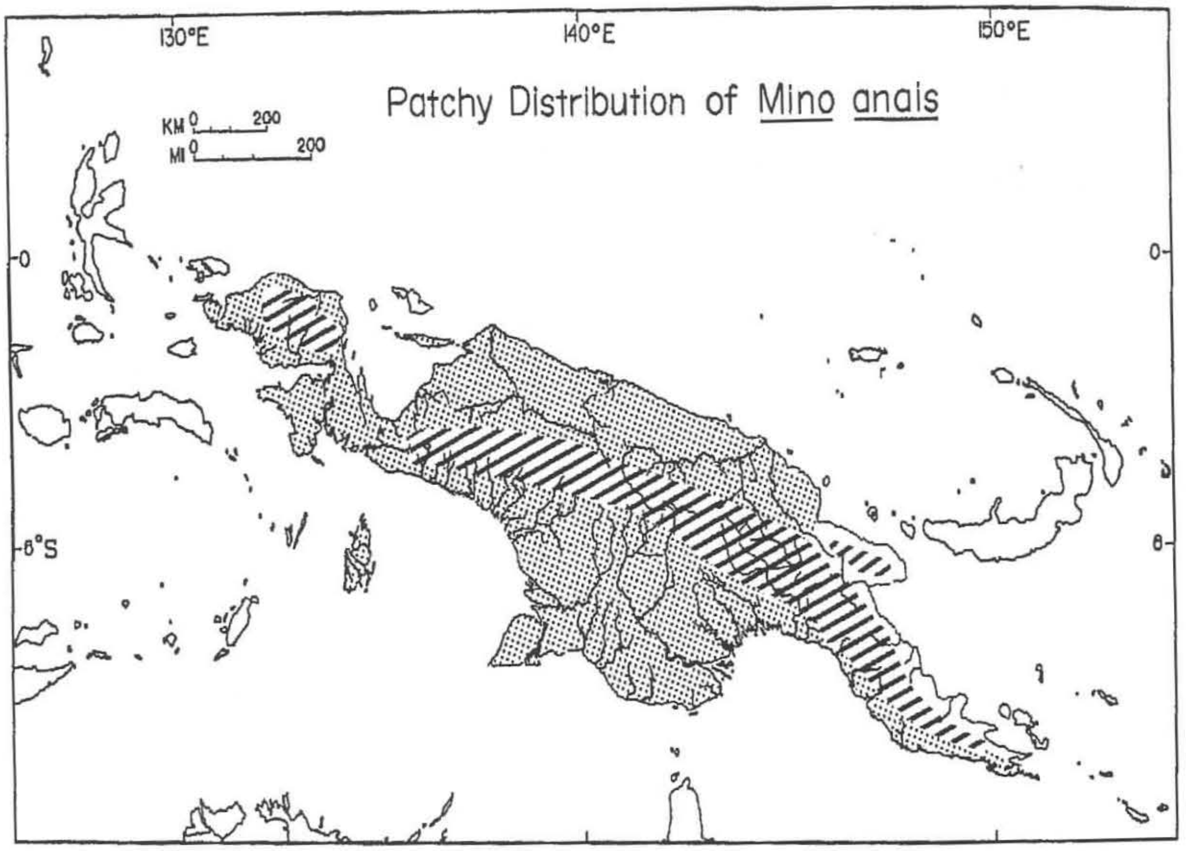
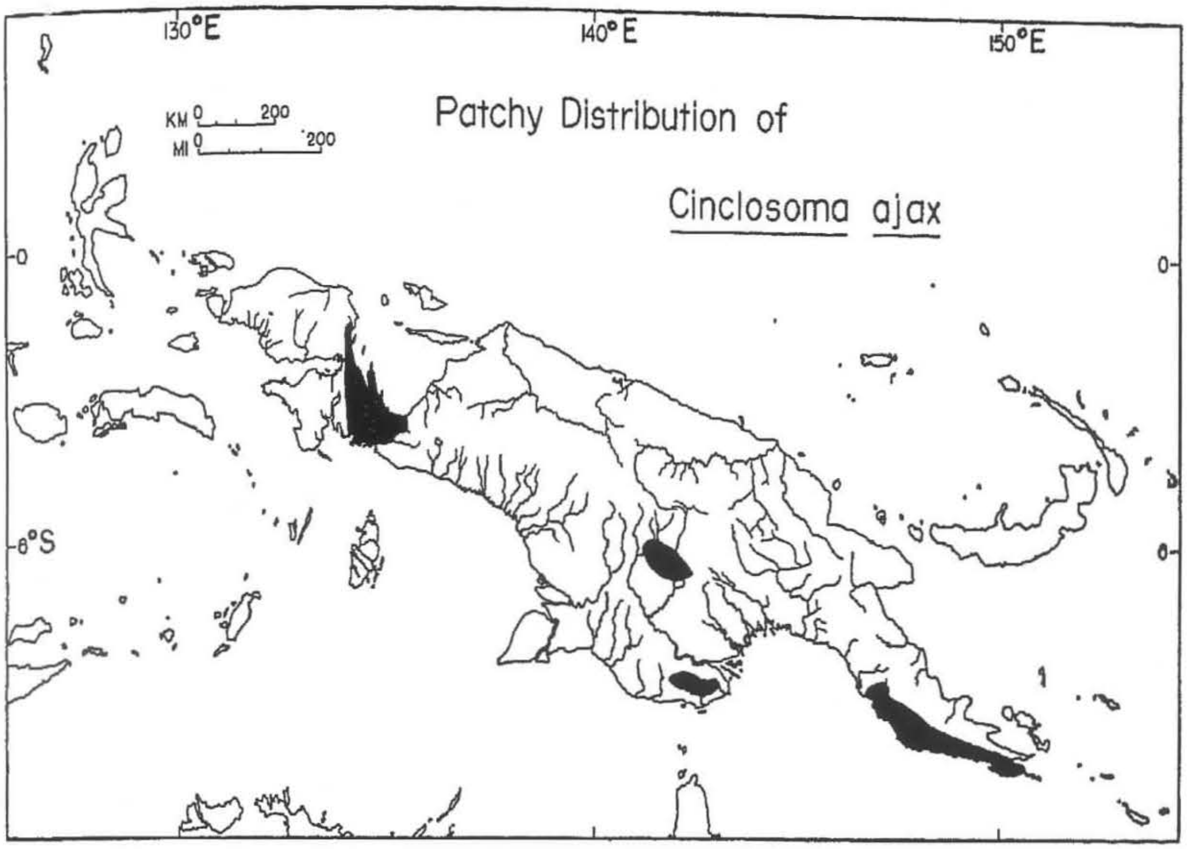


Figure 36 Patchy distribution of the starling *Mino anais* in the lowlands of New Guinea. Areas of occurrence are shaded, and unsuitable mountainous areas are crosshatched. Notice that the species is absent from the lowlands on the northern watershed of southeast New Guinea (unshaded area), despite the presence of suitable habitat, lack of any geographical representative in this area, and continuity of habitat with areas populated by the species.



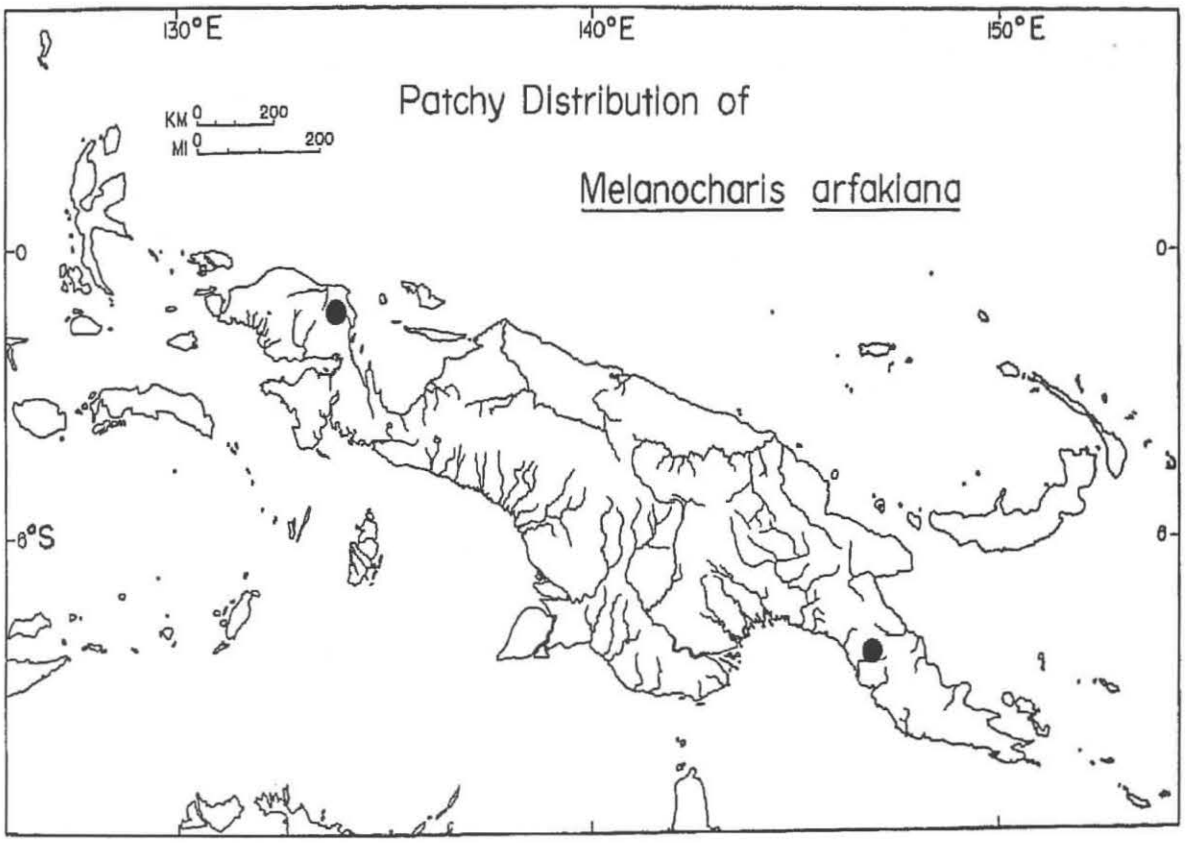


Figure 37 Patchy distribution of the logrunner *Cinclosoma ajax* on New Guinea. The species occurs only in four far-flung areas.

Figure 38 Distribution of the berrypecker *Melanocharis arfakiana* on New Guinea, the ultimate in patchiness. This species is known only from two localities at opposite ends of New Guinea, 1000 miles apart.

Climacteris leucophaea, the sole New Guinea bird in its family, is present in the mountains of eastern and western New Guinea but absent for a distance of 250 miles in the center of New Guinea (Figure 35). The starling *Mino anais* is widespread in the New Guinea lowlands but absent for a distance of 450 miles in northeast New Guinea (Figure 36). The logrunner *Cinclosoma ajax* occurs in four scattered areas of the lowlands (Figure 37). The berrypecker *Melanocharis arfakiana* is known from two localities 1000 miles apart, at opposite ends of the central cordillera (Figure 38). Dozens of similar cases can be cited of conspicuous New Guinea bird species that are present in certain disjunct areas but are absent from hundreds of ecologically similar, ornithologically well-explored localities elsewhere in New Guinea. A skeptic can always dismiss these cases by suggesting that the distributional gaps are deficient in some unspecified but ecologically essential factor. However, many of these cases involve species whose ecological requirements are sufficiently well understood to permit reasonable confidence that their distributional gaps are not due to any feature of the physical environment. This phenomenon of "inexplicably" patchy distributions, i.e., patchy distributions not explicable in terms of habitat conditions, is a distinctive feature of tropical communities compared with temperate communities (MacArthur, 1972, pp. 207-210 and 231–235; Diamond, 1972a, 1973). Many of these distributional patterns may prove to involve species excluded by constellations of competitors, or species that are gradually disappearing and are being outcompeted except on patchy "hot spots". It is suggestive, for example, that the patchily distributed flycatcher *Poecilodryas placens* occurs mainly at localities where its two closest relatives are either both absent, both rare, or only one present.

The problems posed by different species communities in physically similar environments at different localities within the same island, and in physically similar environments on different islands, are formally identical. Both situations involve the question how replicate communities formed from the same species pool can differ. The differences between the inter-island and intra-island situations are two-fold. First, immigration is obviously over water in the former case, over land in the latter. It should not be assumed, however, that dispersal between nearby regions of the New Guinea mainland is much more efficient for New Guinea species than is inter-island dispersal for Bismarck species, since many New Guinea mainland species are highly sedentary. Second, there are more than three times as many species on New Guinea as in the Bismarcks, and a tendency towards patchiness is expected to increase with increasing number of species in the species pool (MacArthur, 1972, pp. 233–234).

Communities at the Habitat Level

So far, we have considered a community as consisting of all the species on a single island, or all the species in a certain geographical area of a large island like

New Guinea. However, within each geographical area, species segregate to varying degrees by habitat. A geographical area consists of a group of habitat communities, close enough to each other so that physical barriers to dispersal are negligible, but each community is still coadjusted in its species composition and is continuously resisting invasion by species of adjacent habitat communities. The assembly of such habitat communities is discussed in detail in Chapter 10 by Cody. Numerous papers in the recent ecological literature have studied "niche shifts" in which the range of habitat communities to which a given species belongs is constricted by competition. Although interpretations in terms of predation or other environmental variables must also be considered in such cases (cf. Connell, Chapter 16), especially for species at lower trophic levels, effects of competition are easiest to recognize when range of habitat occupancy can be related to the presence or absence of a single competitor.

Figure 39 presents a simple example of competitive effects on altitudinal range among three very similar parrots of genus *Vini*. *V. rubronotata* is confined to the New Guinea region, and *V. rubrigularis* to the Bismarcks, while *V. placentis* occurs in both regions. On islands or mountain ranges that *V. placentis* shares with a congener (New Britain shared with *V. rubrigularis*, the North Coastal Range of New Guinea shared with *V. rubronotata*), *V. placentis* is confined to low elevations, the congener to high elevations, and there is little or no altitudinal overlap. On islands or mountain ranges where *V. placentis* occurs alone (Adelbert Range, Mount Karimui, Tolokiwa Island), it spreads upwards to elevations of 4000 feet or higher. On islands or mountain ranges where *V. rubronotata* (Biak Island, Sepik Mountains) or *V. rubrigularis* (Karkar Island) occurs alone, it descends to sea level.

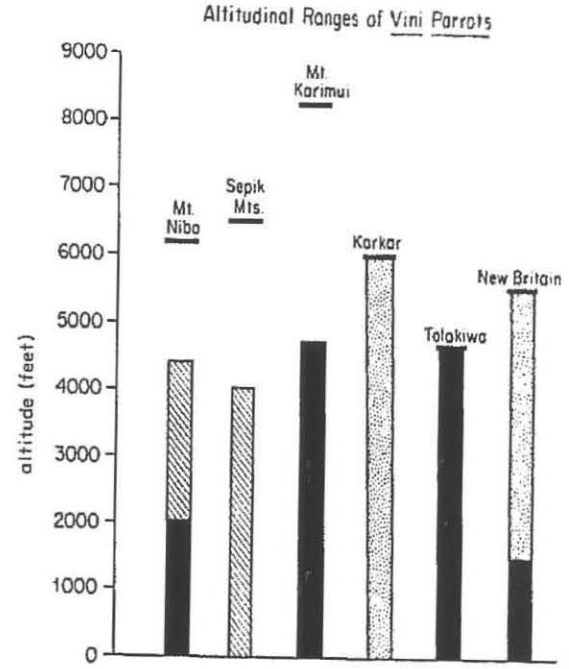


Figure 39 Altitudinal ranges of three similar, congeneric parrots on six mountains of the New Guinea region. Solid shading, *Vini placentis;* diagonal bars, *V. rubronotata;* dots, *V. rubrigularis.* The elevation of the summit of each mountain is indicated by a heavy horizontal bar just under the mountain's name. The left-most three mountains are in different mountain ranges of New Guinea, and the right-most three are separate islands. On mountain ranges or islands where *V. placentis* plus either *V. rubronotata* or *V. rubrigularis* is present, the former is confined to low elevations, the latter to high elevations, with little altitudinal overlap. Where *V. placentis* occurs alone, it ascends to high elevations. Where *V. rubronotata* or *V. rubrigularis* occur alone, they descend to sea level.

Figure 40 is another simple example, demonstrating competitive effects on type of habitat occupied. On New Guinea, as one moves progressively inland from the

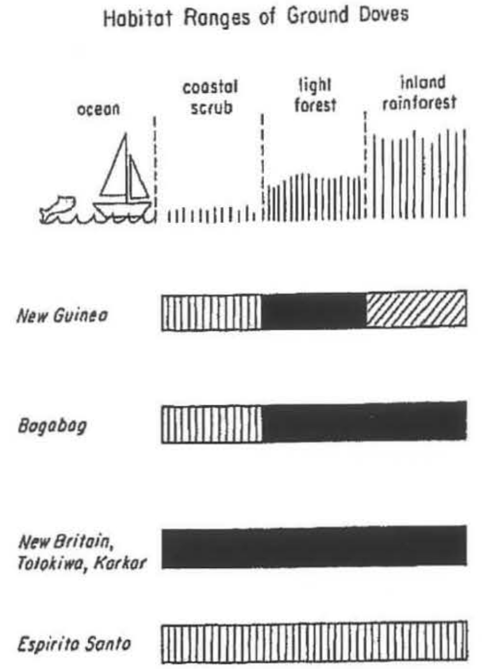


Figure 40 Habitats occupied by three species of ground doves on various islands. As one proceeds inland from the coast on New Guinea, one encounters each species in turn: *Chalcophaps indica* (vertical bars) in coastal scrub, *Chalcophaps stephani* (solid shading) in light forest, and *Gallicolumba rufigula* (diagonal bars) in inland rainforest. On Bagabag, where *G. rufigula* is absent, *C. stephani* expands into inland rainforest. On New Britain, Tolokiwa, and Karkar, where *C. indica* is also absent, *C. stephani* also expands into coastal scrub to occupy the whole habitat spectrum On Espiritu Santo, where only *C. indica* occurs, it occupies the whole habitat spectrum.

coast, from coastal scrub to light forest (or second-growth) to rainforest, one encounters in sequence three similar species of ground doves: *Chalcophaps indica, C. stephani,* and *Gallicolumba rufigula.* On Bagabag, where *G. rufigula* is absent, *C. stephani* expands inland into rainforest. On Karkar, Tolokiwa, New Britain, and numberous other islands where *C. indica* is also absent, *C. stephani* expands coastally to occupy the whole habitat gradient. In the New Hebrides, where *C. indica* is the sole species, it occupies the whole habitat gradient.

A far larger number of cases differ from the neat examples of Figures 39 and 40, in that the geographically varying habitat spectrum occupied by a given species cannot be correlated with the presence or absence of a single competitor. The variation may instead be correlated with changes in a constellation of competitors. Figure 41 illustrates a case that is complex, but out of which some sense, though not yet complete sense, can be made. The figure shows that within the myzomelid-sunbird guild, which we previously discussed at the gross level of whether or not a species occurs on an island, each species may strikingly alter its habitat occupancy from island to island, as a function of what other guild members are present. *Myzomela sclateri* may be ubiquitous (Long), confined to cloud forest (Karkar), or confined to small offshore islets (New Britain); *Nectarinia sericea* may be ubiquitous (Bagabag), only in lowland and midmontane forest (Karkar), only in lowland forest (Umboi), only in coastal vegetation and forest edge (New Britain), or only in forest edge (New Guinea); *Myzomela cruentata* may be confined to montane forest (New Britain), or in lowland forest (Tabar); and *Myzomela cineracea* may be at all elevations in forest (Umboi), only in lowland and mid-montane forest (New Britain, only in lowland forest (widespread New Guinea allospecies), or only in lowland savanna (south New Guinea allospecies). When information about enough islands becomes available, it seems likely that it will be possible to

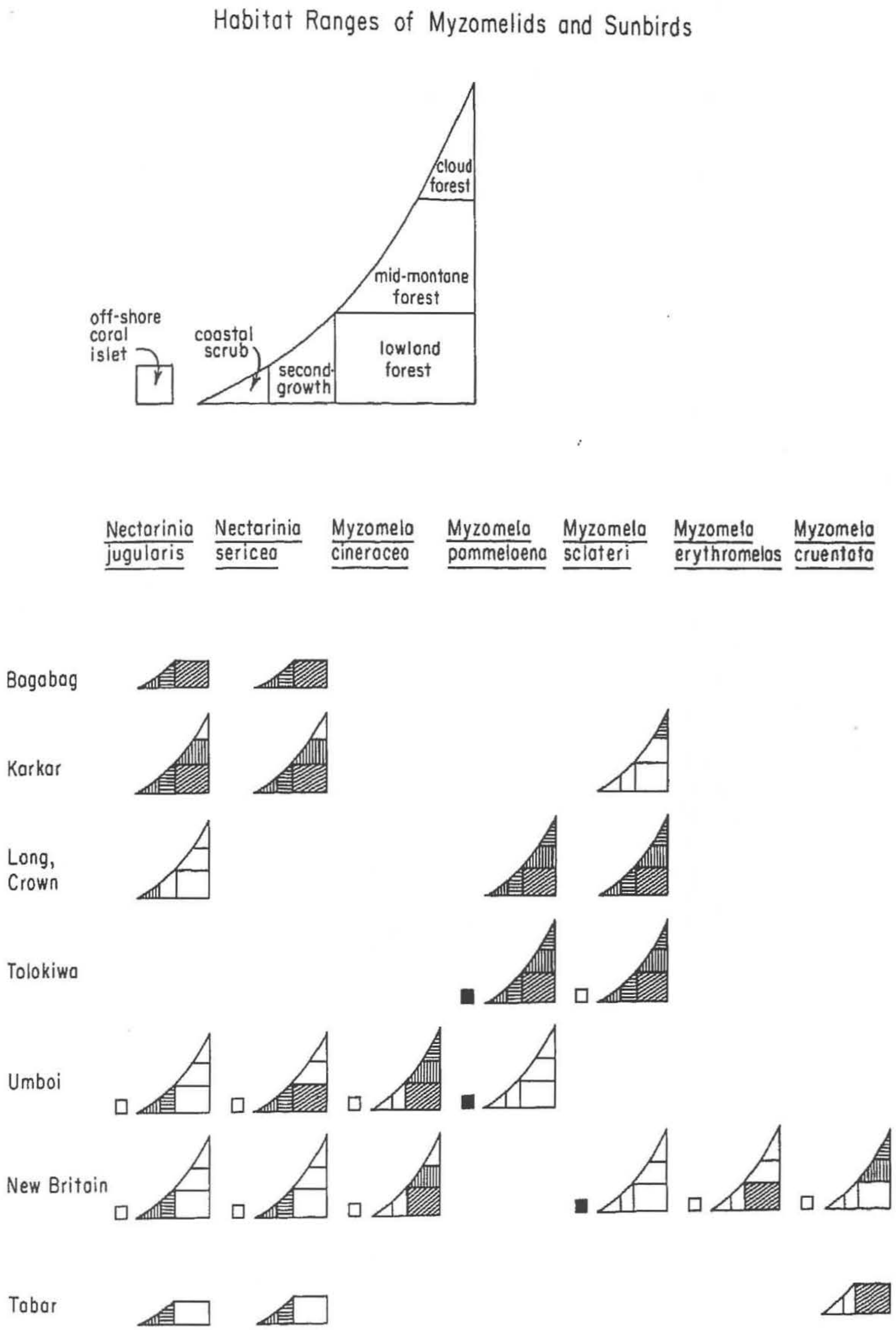


Figure 41 Inter-island variation in habitat partitioning among species of the myzomelid and sunbird guild. The sketch in the upper left shows how the major habitats are pictured. For each island, the habitats occupied by each guild species are shown as variously shaded. Note that the range of habitats occupied by each species varies greatly from island to island, depending on what other species are present. Bagabag and Tabar Islands are not high enough to support midmontane forest or cloud forest.

formulate assembly rules for the subsets of this guild within a habitat. At present the following rules may be tentatively suggested: 1. Two small *Myzomela* species cannot extensively share a habitat. 2. Two large *Myzomela* species cannot extensively share a habitat. 3. The two *Nectarinia* species can extensively share a habitat. 4. One small *Myzomela* species and one large *Myzomela* species can share forest, but cannot share the scrub of a small islet. 5. A small *Myzomela* species can coexist with one but not with both *Nectarinia* species. 6. One *Nectarinia* species can coexist with one small *Myzomela,* but not with one small and one large *Myzomela,* except that *N. jugularis* can sometimes do so precariously in coastal vegetation. Similar assembly rules for habitat subsets can be tentatively formulated for the gleaning flycatcher guild.

Figure 42 illustrates a still more complex case, in which the competition that one species faces is spread even more diffusely over more species. The thrush *Turdus poliocephalus* has a very variable niche. On New Guinea it is confined to the edge of alpine forest and alpine grassland, above 9000 feet. Its habitat on Ceram and probably on Goodenough is similar. On some other islands, such as Bougainville, Guadalcanal, Karkar, and Tolokiwa, it is in montane forest, descending to a lower level that varies between 2460 and 4000 feet. On still other islands, such as Espiritu Santo and Viti Levu, it occurs in forest at all altitudes down to sea level. It also lives on Rennell, a raised coral atoll whose elevation nowhere exceeds 360 feet. Although some of the finer differences may be due to differences in forest physiognomy at a given elevation on islands of different sizes and elevations (the so-called Massenerhebung effect), some other explanation is required for the much grosser differences, given the extraordinary ability of this thrush variously to adapt to alpine grassland, cloud forest, midmontane forest, lowland forest, and coral atolls. The species is equally catholic in its diet (both insects and fruit), so that it will be difficult to delimit its guild and identify a critical constellation of competitors. However, a suggestive clue is that on any Pacific island the number of species decreases with increasing elevation, and that a forest community with a given number of species may therefore be encountered at sea level on a species-poor island but only at much higher elevations on a species-rich island. As indicated on Figure 42, the maximum number of species in the habitat communities occupied by *Turdus poliocephalus* on each island shows much less inter-island variation (23 to 36 species) than does the number of total species on each island (42 to 513). By analogy, then, with incidence functions such as Figures 6 below, 14, and 15, one can describe *Turdus poliocephalus* as a supertramp with an upper S_{crit} in the range 23–36, capable of invading only those habitat communities with this number of species or fewer.

Competitive effects similar to the effects on habitat range illustrated in Figures 40 and 41, and similar to the effects on altitudinal range illustrated in Figures 39 and 42, also exist for vertical foraging range. An example of simple effects involving

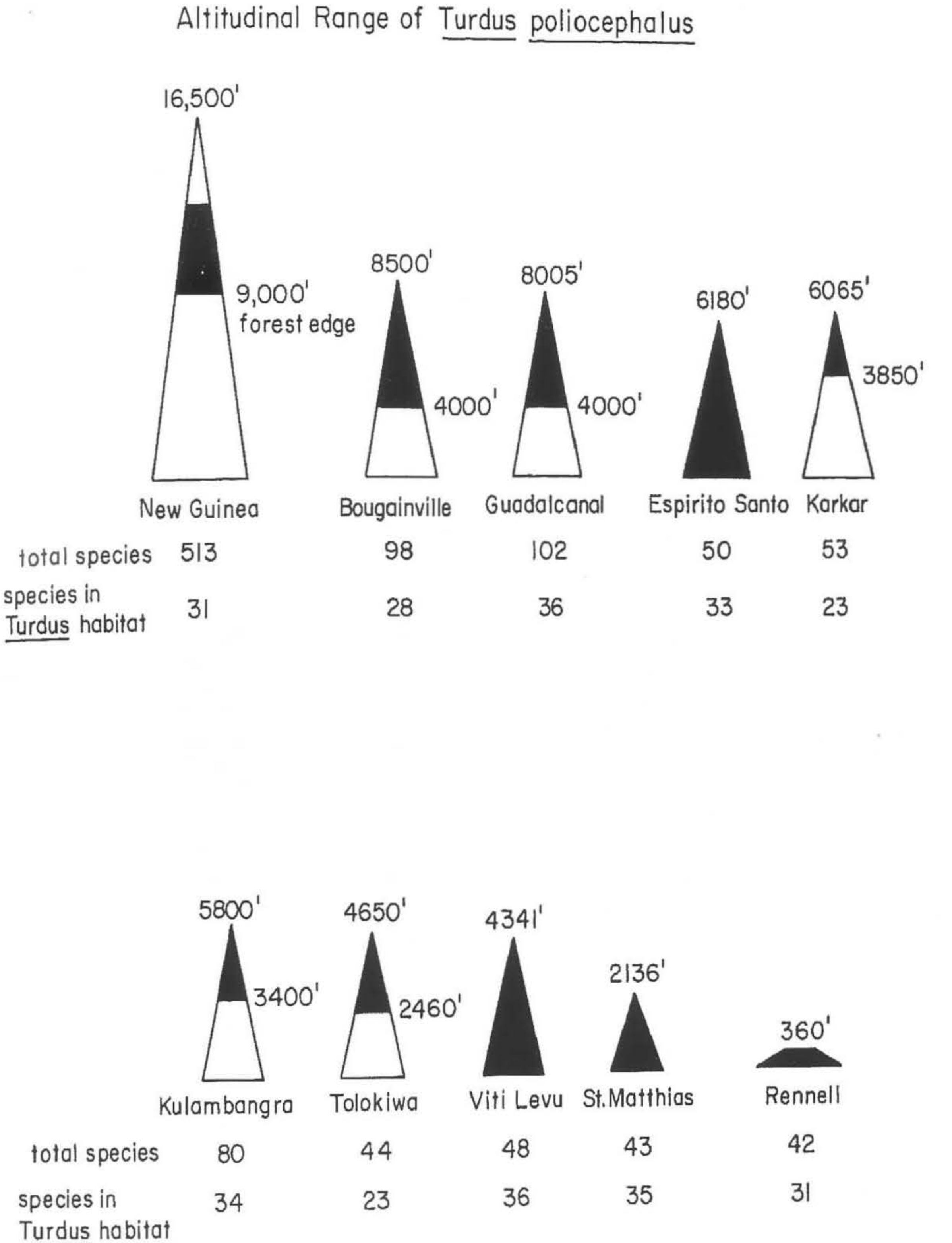


Figure 42 Interisland variation in altitudinal range of the thrush *Turdus poliocephalus.* For each island the numbers represent the total number of bird species on the island, the number of bird species in the habitat occupied by *Turdus poliocephalus,* the highest elevation on the island (written above the island pyramid), and the lower altitudinal limit of *Turdus poliocephalus* (if this species does not descend to sea level); the altitudinal range inhabited by *Turdus poliocephalus* is shaded. *Turdus* lives in forest and/or scrub on all islands except New Guinea, where it lives mainly at the edge between forest and alpine grassland. On each island it adjusts its altitudinal range or habitat preference so as to encounter a fauna of about the same richness (23–36 species). In more detail, it can encounter more species (31–36) on islands without the thrush-like insectivorous ground birds called pittas (Guadalcanal, Kulambangra, Espiritu Santo, Viti Levu, St. Matthias, Rennell) than on islands with pittas (23–31 species: New Guinea, Bougainville, Karkar, Tolokiwa), because pittas may be disproportionately important competitors of *Turdus poliocephalus.* This may underlie the different altitudinal ranges on Espiritu Santo vs. Karkar, or on Tolokiwa vs. Viti Levu, the two islands of each pair being otherwise similar in total species number and maximum elevation.

one or two readily identifiable competitors, analogous to Figures 39 and 40, is provided by the flycatchers *Pachycephala hyperythra* and *P. soror.* Where these species coexist on the central cordillera of New Guinea, *P. soror* spends much time in the understory and is often caught in mist-nets, whereas *P. hyperythra* remains 10 or more feet above the ground and is seldom or never netted. In the North Coastal Range of New Guinea, where *P. soror* is absent, *P. hyperythra* often utilizes the understory and is regularly netted. A more complex case analogous to Figure 42, in that numerous, more distantly related competitors are involved, is provided by the omnivorous cuckoo-shrike *Lalage leucomela.* On New Guinea (total number of bird species, 513) it is confined to the tree crowns; on New Britain (127 species) it occasionally descends to the lower story; and on Espiritu Santo (50 species) and Samoa (28 species) the related species *L. leucopyga* and *L. maculosa,* respectively, descend to the ground (see Figure 43).

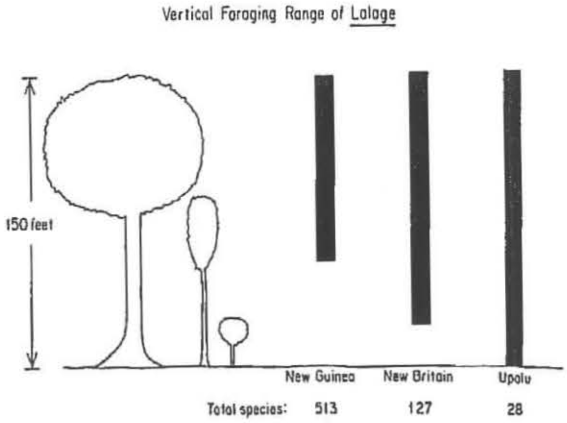


Figure 43 Inter-island variation in vertical foraging range of *Lalage* cuckoo-shrikes. On New Guinea, with a total of 513 bird species, *Lalage leucomela* is confined to the crowns; on New Britain, with 127 species, it occasionally descends to shrub level; and on Upolu (Samoa), with 28 species, the related *L. maculosa* regularly descends to the ground. Evidently the vertical foraging range is compressed on species-rich islands by diffuse competition.

In general, the ease with which we were able to construct assembly rules for guilds on islands was inversely proportional to the number of species in the guild, and directly proportional to the ecological isolation of the guild from other guilds. The same factors determine the ease with which we can understand patchy distributions (Figures 35–38) or competitive effects on spatial niche parameters (Figures 39–43). If most of the competition faced by a particular species comes from just one or two other species, we stand a good chance of being able to construct assembly rules for island communities (e.g., Table 7), to recognize what fills the missing patches (e.g., Figures 33 and 34), or to construct assembly rules for habitat communities (e.g., Figure 41). If instead there is diffuse competition from many species and no single competitor is overwhelmingly important, we remain baffled by patchiness (Figures 35–38), and we can make only statistical predictions of the probability that a species will occur on a particular island, from total species number and incidence functions. The cases of *Lalage* (previous paragraph) and *Turdus poliocephalus* (Figure 42) suggest the possibility that statistical predictions of diffuse competitive effects on spatial niche parameters could similarly be obtained, by constructing graphs analogous to incidence functions. These graphs would have total species number on an island as the abscissa, and the spatial limit of a particular species' range (highest or lowest altitude, vertical foraging height, or position on habitat gradient) as the ordinate.

The Origin of Assembly Rules

Community assembly involves the following patterns:

> If one considers all the combinations that can be formed from a group of related species, only certain ones of these combinations exist in nature.
>
> Permissible combinations resist invaders that would transform them into forbidden combinations.
>
> A combination that is stable on a large or species-rich island may be unstable on a small or species-poor island.
>
> On a small or species-poor island, a combination may resist invaders that would be incorporated on a larger or more species-rich island.
>
> Some pairs of species never coexist, either by themselves or as part of a larger combination.
>
> Some pairs of species that form an unstable combination by themselves may form part of a stable larger combination.
>
> Conversely, some combinations that are composed entirely of stable subcombinations are themselves unstable.

Let us now attempt to understand assembly rules in terms of resource utilization, overexploitation strategies, dispersal strategies, and transition probabilities between species combinations.

Resource Utilization

It seems likely that competition for resources is a major factor underlying assembly rules. Permissible combinations of species may often be those combinations (out of all the combinations containing the same total number of species) that leave the fewest resources unutilized, that are therefore relatively immune to displacement of one component species by an invading species, and that still provide each component species with enough resources to maintain a stable population. A full analysis of how the species of a guild are coupled to each other through utilization of resources requires knowledge of the so-called utilization function U of each species, taking account of the multidimensionality of U's, the differences in compressibility of U's along different resource axes, and the relative ability of each species to displace each other species from each portion of resource space. We shall discuss the principles involved in such an analysis and then apply them to the fruit-pigeon guild.

We begin by considering one-dimensional incompressible U's, for illustrative purposes. Suppose that the biologically important differences in the resources harvested by different species of a guild—i.e., the differences that enable the species to coexist—can be described in terms of one resource variable, x. (An example would be the diameter of fruit eaten by *Ptilinopus-Ducula* fruit pigeons in the same habitat, but these pigeons segregate along a tapering tree branch as well as along a fruit-diameter axis (Figure 30). A better example would be altitude in the case of the trios and quartets of New Guinea bird species that strictly segregate by altitude (cf. Diamond, 1972a, pp. 27-35 and p. 217; 1973)). Then the frequency distribution $R(x)$ of resource production available to the guild can be plotted along one axis. The frequency distribution of resources consumed by each individual of each species, the utilization function $U(x)$ of the species, can be plotted along the same axis (Figure 44). The total resource production available to the guild is $\int_x R(x)dx$; the resources consumed by the n_i individuals of each species i present are $n_i \int_x U_i(x)dx$; the frequency distribution of unutilized resource production $V(x)$ is given by

$$V(x) = R(x) - \sum_i n_i U_i(x) \qquad (8)$$

and $\int_x V(x)dx$ is the total production of unutilized resources. Depending upon the forms of all the functions $U_i(x)$, $\int_x V(x)dx$ will in general be lower for certain combinations of species than for others. Combinations with high $\Sigma n_i \int U_i dx$ and low $\int V(x)dx$ will maintain higher populations, and will leave fewer resources that could support an invader, than combinations with the reverse properties. Assuming that $\int R(x)dx$ is proportional to island area, and that (for a given combination of species) the n_i's are also proportional to area, then $\int V(x)dx$ will also be proportional to area. Thus, the resources left unconsumed by a certain combination of species may be too small to support a stable population of an additional species if the island is small, but may be sufficient to support an additional species if the island is larger.

For example, consider the four-species guild depicted in Figure 44a. The only species that could maintain a stable population on the small island whose production curve is depicted on the left of Figure 44b would be species 3. On a somewhat larger island (Figures 44c and 44d) species 2 and 4 could both persist together, would be preferred over species 3 alone by virtue of leaving fewer unutilized resources, and would leave too few resources for either species 1 or 3 to coexist in addition. On a still larger island (Figure 44e) species 1 could maintain itself along with species 2 and 4. Thus, Figure 44 suggests explanations for many of the findings listed at the beginning of the section "The origin of assembly rules": that certain combinations of n species are preferred over others (e.g., in Figure 44e, species $1 + 2 + 4$ preferred over $2 + 3 + 4$); that permissible combinations resist certain invaders (e.g., species $2 + 4$ resist species 3 in Figure 44d); that a combination stable on a small island may be unstable on a large island (e.g., species 3 stable in Figure 44b, unstable in Figure 44c–44d); that, conversely, a combination stable on a large island may be unstable on a small island (e.g., species $1 + 2 + 4$ are stable in Figure 44e but not in 44d); that, correspondingly, invaders resisted by a combination on a small island may be incorporated on a large island (e.g., species $2 + 4$ incorporate species 1 in Figure 44e but not in 44d); and that combinations composed entirely of stable subcombinations may be unstable (e.g., species $2 + 4$ stable, species 3 stable, species $2 + 3 + 4$ unstable).

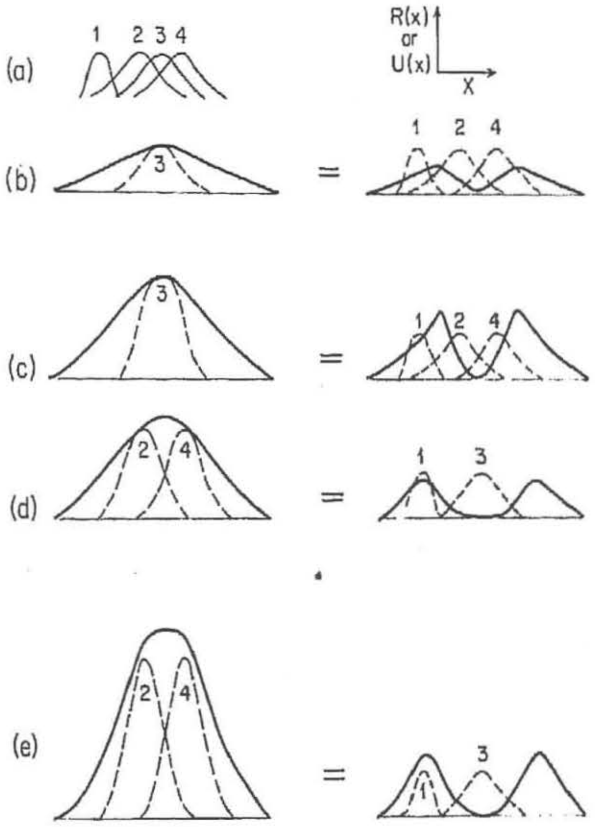


Figure 44 Illustration of how the match of utilization functions $U(x)$ to resource production curves $R(x)$ could help explain why certain combinations of species occur in nature and others do not. Resource production is assumed to be distributed along a single dimension (e.g., fruit size or altitude) according to curves such as the solid curves on the left of Figures 44b–44e. Each of four species i has a characteristic utilization function or frequency distribution of resources consumed, illustrated by the four curves of Figure 44a. The areas under these curves, $\int U_i(x)dx$, represent the resource production rate required for maintaining the smallest population of each species that could survive for a reasonable length of time. Thus, multiplying the ordinate values of each $U_i(x)$ by M_i yields a population M_i times the minimum size. The left sides of Figures 44b–44e all depict curves $M_iU_i(x)$ that fit entirely under the illustrated $R(x)$ but are still greater than 1.0 times $U_i(x)$, meaning that the illustrated $R(x)$ is sufficient for species i to maintain a stable population on the island. The right sides of Figures 44b–44e give as solid curves $R(x) - \Sigma M_iU_i\ (x)$, i.e., the unutilized resource distribution $V(x)$; the dashed curves represent 1.0 times $U_j(x)$ for species j that do not fit under the $V(x)$ curve and hence cannot maintain stable populations on the island in coexistence with species i. In Figure 44b (left) only 1.0 $U_3(x)$ [i.e., 1.0 times $U_3(x)$] fits under $R_b(x)$, and 1.0 $U_1(x)$, 1.0 $U_2(x)$, or 1.0 $U_4(x)$ would not. $R_b(x) - 1.0\ U_3(x)$ equals $V_b(x)$, the solid curve on the right; $U_1(x)$, $U_2(x)$, and $U_4(x)$ all exceed $V_b(x)$. Thus, none of these three species could maintain itself alone on this island nor share the island with species 3. Figure 44c represents an island whose area is double that of the island of Figure 44b, so that $R_c(x)$ is twice as high as $R_b(x)$, and twice as large a population of species 3 can be maintained (dashed curve 2.0 $U_3(x)$ on the left). On the right, $R_c(x) - 2.0\ U_3(x) = V_c(x)$; this exceeds 1.0 $U_2(x)$ or 1.0 $U_4(x)$ and barely exceeds $U_1(x)$, so that species 1 might be marginally capable of sharing this island with species 3, but species 2 or 4 could not. Figure 44d depicts the same island as Figure 44c, so that $R_d(x) = R_c(x)$; 1.9 $U_2(x)$ or 1.9 $U_4(x)$ fit under $R_d(x)$, alone or summed, so that these two species can coexist on this island. On the right $R_d(x) - 1.9\ U_2(x) - 1.9\ U_4(x) = V_d(x)$; this exceeds 1.0 $U_3(x)$ and barely exceeds $U_1(x)$. Since the area under the curve $V_d(x)$ is less than the area under $V_c(x)$, species 2 and species 4 together leave fewer unutilized resources on this island than species 1 and are more likely to occur. Figure 44e represents an island four times as large as that of Figure 44b, with $R_e(x)$ four times as high as $R_b(x)$. The maximum value of M such that $R_e(x) - MU_2(x) - MU_4(x) \geq 0$ for all x is now 3.8, so that this island can simultaneously support populations of species 2 and 4 that are 3.8 times the minimum size (dashed curves on left). On the right $R_e(x) - 3.8\ U_2(x) - 3.8\ U_4(x) = V_e(x)$; this exceeds 1.0 $U_1(x)$ but is less than 1.0 $U_3(x)$, so that species 1 but not species 3 could share this island with species 2 and 4. Thus, in this guild one would usually find species 3 on a small island, species 2 + 4 or occasionally 1 + 3 on a larger island,

More realistically, U's and R's are multidimensional and involve spatial variables (habitat type, altitude, and vertical height above the ground) and variables related to foraging behavior as well as food variables. For example, among New Guinea frugivorous pigeons (including not only the fruit pigeons of the genera *Ptilinopus* and *Ducula* but also cuckoo-doves, ground doves, and some other groups) the most significant food variables are size and hardness of fruit. Among flycatchers, variables related to foraging behavior include gross foraging technique (gleaning, sallying, hovering, etc.) and quantitative foraging characteristics (ratio between stationary and moving time, duration of stationary or moving bouts, and rate of travel). Other examples of significant resource axes include calendar time (for butterflies: Shapiro, Chapter 8), seed size and microhabitat (for desert rodents: Brown, Chapter 13), clock time, microhabitat, and food type (for desert lizards: Pianka, Chapter 12), prey size, prey type, foraging tactic, and foraging zone (for oak-woodland insectivorous birds: Hespenheide, Chapter 7), and position on habitat gradient (for Mediterranean birds: Cody, Chapter 10).

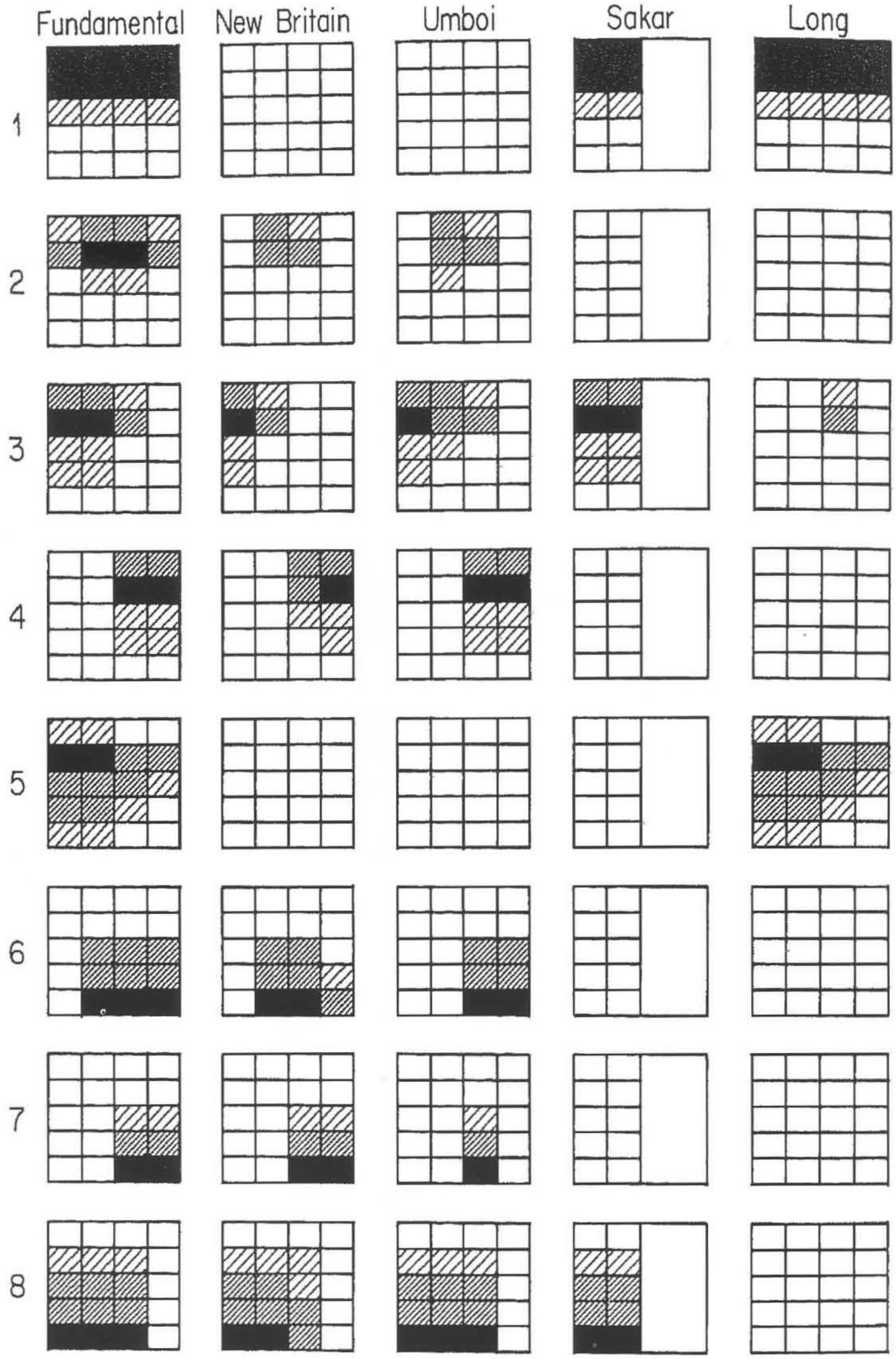
A further important property of real U's is that they are compressible under competition, and are much more compressible along certain axes than along other axes. When a species shifts from a species-poor fauna to a species-rich fauna, its U is often found to become compressed along spatial axes but rarely along axes related to foraging tactics (Crowell, 1962; Diamond, 1970a, 1970b, 1973). This spatial compressibility has been illustrated in Figures 39–43. For this reason measurements of so-called α's or niche overlaps (cf. Chapter 13, Brown; Chapter 7, Hespenheide; and Chapter 12, Pianka) may provide good estimates of competition coefficients for dimensions along which U's are relatively incompressible, but may give not even the crudest approximation to competition coefficients along spatial axes. For example, strict spatial segregation between two species means that along a spatial axis the niche overlap is 0, but it may also mean that this is precisely because the competition coefficient for the fundamental niches is close to 1.0. If one measures the fundamental niches of several related species in each other's absence and finds the niches to overlap in some portion of niche space, then prediction of assembly rules may require knowing two further properties of each species, both as a function of position in niche space: the relative resource-harvesting rate as a function of resource density (see section "Companions in starvation"), and the ability to displace other species by aggressive behavior.

The simplest application of U's to understanding assembly rules is to the members of incompatible pairs or sets, the closely related species that are of similar size and foraging technique and never coexist on an island (cf. *Macropygia mackinlayi* and *M. nigrirostris*, Figure 20, Table 9, and the small lowland myzomelids, Figure 23). These are species whose U's of the fundamental niche must overlap so broadly that there is no way for the two species to divide an island spatially such that each species has a significantly higher fundamental *U* than the other in some habitat. Within these incompatible pairs or sets, the high-*S* or tramp species has the advantage on large islands because of its ability to overexploit and tolerate low resource levels, while the supertramp has the advantage on small or remote islands because of its high dispersal rates and reproductive potential (see section "Companions in starvation"). Much more often, however, species whose *U*'s are very similar along nonspatial axes differ sufficiently along some spatial axis that they can coexist on an island by segregating spatially. For instance, the fruit size distributions of the similar-sized pigeons *Ducula melanochroa* and *D. rubricera* are very similar (curves labeled 661 g and 722 g, upper half of Figure 31), but all islands on which *D. melanochroa* lives are nevertheless shared with *D. rubricera,* the former species being concentrated in the mountains, the latter in the lowlands. Other habitat vicariants of similar size presumably also have similar *U*'s along axes other than some spatial axis.

In the remainder of this section let us consider in detail the Bismarck fruit-pigeon guild, the case in which we can come the closest to reconstructing assembly rules from inter-island competitive shifts in resource utilization along more than one dimension. We can compact this system to two dimensions, because all the species live in the canopy, eat soft fruit, and pick fruit in the same manner; the habitat dimension and altitude dimension can be combined into one axis; and the remaining axis is taken as fruit size, with which the microhabitat dimension (diameter of branch used as perch) is directly correlated, since both are related to pigeon body size. For simplicity of graphical representation in preference to utilization contours in this two-dimensional space, Figure 45 displays more coarsely the utilization function of each of eight common pigeon species on each of four islands: each axis is quantized into four or five values, and shading on the resultant checkerboard (quantized in three values) indicates intensity of utilization. The left-most column of checkerboards approximates the fundamental niche by depicting the utilization function of each species on the most species-poor Bismarck island where it occurs, but even this underestimates the fundamental niche in most cases; *Ducula finschii* and *D. melanochroa,* for instance, occur only on islands with at least six species of fruit pigeons. Figure 45 yields the following conclusions:

(a) The fundamental niches of the eight species overlap massively (compare corresponding squares in the first column of eight checkerboards entitled "fundamental"). One square of the niche-space checkerboard may be utilized by up to six species, resulting in up to 537 units of utilization (see Figure 45 legend for definition).

(b) Rarely does a species achieve its fundamental niche on an island. Instead, the realized utilization functions are considerably compressed, as may be seen by comparing the left-most checkerboard in any row with the other four checkerboards. For instance, *Ptilinopus insolitus* (third row of checkerboards) underutilizes the lowland forest of Umboi (compare



(a)

shading in second column of its Umboi and fundamental checkerboards), underutilizes lowland forest and is absent from hill forest on New Britain, and is absent from second-growth and lowland forest and confined to hill forest on Long, Tolokiwa, and Crown. Since we have underestimated fundamental niches because we could not study each species in the absence of the other species, we have also underestimated the degree of compression.

(c) The compressions of various species on the same island are correlated, in a way such that no square of the niche-space checkerboard on an island is actually utilized by more than four species or receives more than 353 (usually not more than 240) units of utilization. Conversely, except on Long (plus Tolokiwa and Sakar), no square receives less than 75 units of utilization. [Utilization drops to 9–42 units for large fruit in the hills and mountains of Long, as reflected in the fact that the largest pigeon of Long (*Ducula pistrinaria*) weighs only 470 g and it becomes uncommon at higher elevations.] Some qualitative examples of how this distribution of utilization is achieved through selection and compression of colonists deserve notice before we consider a quantitative analysis. The medium-large supertramp *Ducula pistrinaria* (species 5 of Figure 45), which has sent colonists to all the islands of Figure 45 (and undoubtedly to all other Bismarck islands), is established on Long, but on the three other islands of Figure 45 it is "squeezed out" between some combination of the large species 7 and 8, the similar-sized species 6, and the

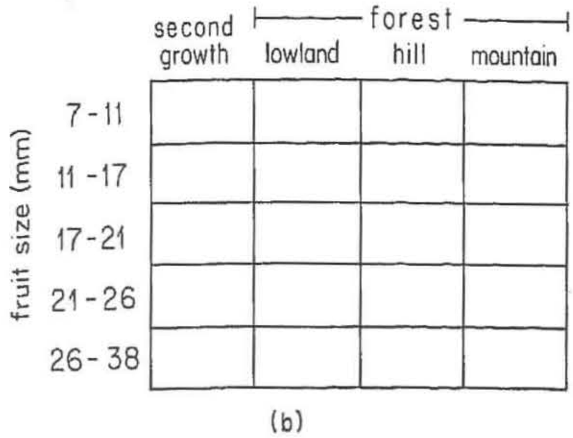


Figure 45 Assembly of the fruit-pigeon guild on some Bismarck islands. Each of the 40 checkerboards (a) represents the resource utilization of one fruit-pigeon species on one island, in a two-dimensional niche space. As shown in the enlarged checkerboard (b) giving the key to the 20 squares of each checkerboard, the ordinate of each checkerboard is a fruit-size axis divided into five intervals, and the abscissa is a habitat-plus-altitude axis divided into four intervals. The shading of each of the 20 squares of each checkerboard indicates how heavily the given species utilizes the given portion of niche space on the given island: solid shading = heavy use, close diagonal bars = moderate use, sparse diagonal bars = light use. Utilization units were calculated by rating abundance of the species in the habitat as 0 (absent) 1, 2, or 3 (abundant), and by multiplying this abundance value times the percentage of fruit in the diet that fell within the given size range, obtained from graphs similar to Figure 31 above. A product of ≥ 100, 40–99, and 20–39 was equated with heavy, moderate, and light use, respectively. For instance, in hill forest on New Britain *Ptilinopus rivoli* was fairly common, abundance rating 2; 44% of the fruit it consumed was in the size range 11–17 mm; hence the utilization product in this square of niche space (second row and third column of the checkerboard in the fourth row (species "4") and second column ("New Britain") of checkerboards) is 88, construed as moderate use and depicted by close diagonal bars. The species, coded by the eight numbers to the left of each row of checkerboards, are: 1 = *Ptilinopus solomonensis* (91 g), 2 = *P. superbus* (123 g), 3 = *P. insolitus* (144 g), 4 = *P. rivoli* (135 g), 5 = *Ducula pistrinaria* (470 g), 6 = *D. finschii* (383 g), 7 = *D. melanochroa* (661 g), 8 = *D. rubricera* (722 g). The second through fifth columns of checkerboards represent the single island named at the top of the column; the left-most column depicts the niche of the species on that Bismarck island (not necessarily one of the four depicted) where the species encounters the fewest other fruit-pigeon species; this is taken as an approximation of the fundamental niche. Utilization on Tolokiwa and Crown is virtually identical to utilization on Long. Hill forest and mountain forest were not studied adequately on Sakar. See text for discussion.

medium-small species 2 and 3. The small supertramp *Ptilinopus solomonensis* (species 1), which is ubiquitous on Long as a consumer of 7–17-mm fruits (first two rows of each checkerboard), is replaced in this capacity on New Britain and Umboi by three habitat specialists: *P. insolitus* (species 3) in second-growth and lowland forest, *P. superbus* (species 2) in lowland forest and hill forest, and *P. rivoli* (species 4) in hill forest and mountain forest. The medium-small *P. insolitus* (species 3), which mainly eats fruit in the range 11–17 mm, shares both Sakar and Long with the small *P. solomonensis* (species 1, mainly 9–14-mm fruit), but differs strikingly from island to island in habitat preference: ubiquitous on Sakar, confined to hill forest on Long (plus Tolokiwa and Crown), and squeezed out of hill forest by the combination of the similar-sized *P. superbus* and *P. rivoli* on New Britain. To an ornithologist who has learned *P. insolitus* as the second-growth small fruit pigeon of New Britain, this inversion of its habitat preference on Long is astonishing. The reason for the difference between Sakar and Long is that the remaining species of Sakar besides *P. insolitus* and *P. solomonensis,* the very large *D. rubricera* (species 8), eats mainly 22–30-mm fruit, leaving much medium-sized fruit to support a medium-small pigeon; but the remaining species of Long, the medium-large *D. pistrinaria* (species 5), eats mainly 15–21-mm fruit, squeezing out *P. insolitus* between *D. pistrinaria* and *P. solomonensis* except in hill forest, where *D. pistrinaria* becomes less common.

Thus, Figure 45 probably illustrates *how communities are assembled through selection of colonists, adjustment of their abundances, and compression of their niches, in part so as to match the resource consumption curve of the colonists to the resource production curve of the island.* For a quantitative test of this hypothesis, we need both the consumption curve and the production curve. The form of the consumption curve is available from analyses of stomach contents as expressed in Figure 31, combined with the relative abundances and habitat distributions of each species. The production curve is unfortunately difficult to measure and is unknown; we assume, however, that it will be roughly bell-shaped, and observation suggests that there is relatively more large fruit in the lowlands than in the mountains. We can therefore proceed by (a) constructing consumption curves of actual pigeon communities, (b) comparing the shapes of these curves with the expected shapes of production curves, and (c) comparing the actual consumption curves with those calculated for imaginary communities of forbidden combinations of species.

Figure 46 depicts the actual consumption curves for the fruit-pigeon combinations in the lowlands of Sakar, in the lowlands of Long, and in the mountains of Long. These curves were constructed by summing the products of single-species consumption curves such as Figure 31 times the relative abundance of each species in the given habitat. All three curves are approximately bell-shaped. The curves for the Long and Sakar lowlands are quite similar, especially in the range of small fruit; slightly more large fruit and

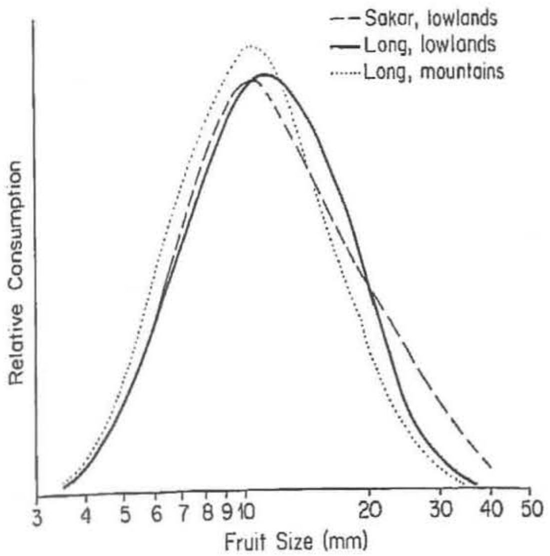


Figure 46 Actual consumption curves for the fruit-pigeon guild in the lowlands of Long Island and Sakar Island and at an elevation of about 1500 feet in the mountains of Long. The ordinate is the relative consumption (arbitrary units), by all species of the guild present, of fruit of the diameter given by the abscissa (logarithmic scale). To obtain these local-guild consumption curves, the frequency distribution of fruit sizes in the stomach of each species present was measured as in Figure 31 and was weighted by the relative abundance of the species. The three curves were then scaled to give approximately the same area. Relative abundances are: Long lowlands, *Ptilinopus solomonensis: Ducula pistrinaria*, 60:40; Long mountains, *P. solomonensis: P. insolitus: D. pistrinaria*, 77: 9: 15; Sakar lowlands, *P. solomonesis: P. insolitus: D. rubricera*, 43: 29: 29. Curves for Tolokiwa and Crown Islands are very similar to those for Long. Note that all three curves are bell-shaped (as one would expect for the distribution of fruit production), that the two lowland curves are quite similar, and that the curve for the mountains of Long is slightly shifted towards smaller fruit.

less medium-sized fruit are consumed on Sakar than on Long. The curve for the Long mountains is shifted somewhat towards small fruit (more consumption of small fruit and less of large fruit). Thus, it is at least possible that the actual consumption curves provide good matches to production curves.

We can now fit the actual consumption curves of Figure 46 to curves calculated for other combinations of species. Figure 47 compares the actual lowland curves to the curve of *P. solomonensis* (91 g) + *D. rubricera* (722 g), the smallest and the largest species of Figure 45; the ratio of their abundances (2.0 : 1.0) is chosen so as to give the best fit to the actual curves. This combination of species exists on no Bismarck island. Compared with the actual curve for Sakar [*P. solomonensis* (91 g) + *P. insolitus* (144 g) + *D. rubricera* (722 g) in the proportions 1.5 : 1.0 : 1.0], the imaginary combination fits well in the fruit-size range above 12 mm but consumes too much small fruit. In effect, the actual presence of an additional medium-small species on Sakar lets the otherwise excessive consumption of small fruit be eliminated by reducing the *P. solomonensis*/*D. rubricera* ratio without at the same time developing a deficit in consumption of medium-small (11–17-mm) fruit. Compared to the actual curve for Long [*P. solomonensis* (91 g) + *D. pistrinaria* (470 g), proportions 1.5 : 1.0], the fitted combination consumes too much large fruit (because of the replacement of *D. pistrinaria* with the larger *D. rubricera*) and too little medium-small fruit but too much small fruit (because the small *P. solomonensis* in the imaginary combination is in effect trying to eat alone what it actually eats together with the medium-sized *D. pistrinaria* on Long). Figure 48 compares the actual lowland curves to the best-fit combination of *P. insolitus* (144 g) + *D. rubricera* (722 g) (proportions 2.0 : 1.0). This

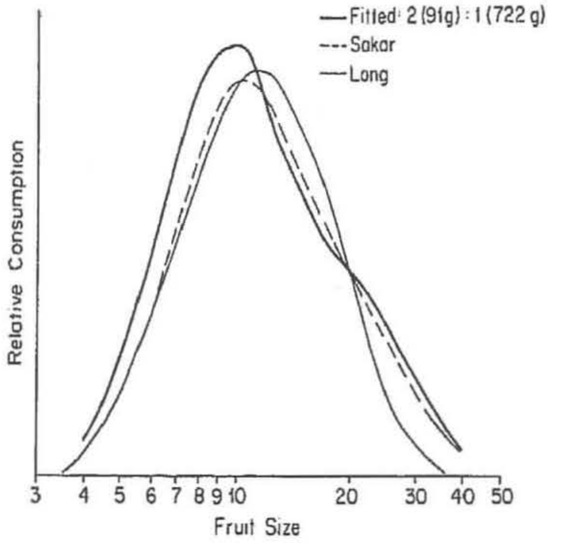


Figure 47 Comparison of actual and fitted consumption curves by combinations of fruit pigeons. The curves labeled "Sakar" and "Long" are the actual curves for the guilds present in the lowlands of these islands, copied from Figure 46. The "fitted" curve was calculated for the imaginary combination of *P. solomonensis* (91 g) and *D. rubricera* (722 g) from the single-species consumption curves of Figure 31 below, with the abundance ratio adjusted to 2:1 to give the best fit to the two actual curves. Note that the fitted curve for the imaginary combination utilizes more small fruit of <11 mm diameter than the actual guilds on either island, and utilizes less medium-sized fruit and more large fruit than the actual guild on Long. The combination *P. solomonensis* and *D. rubricera* actually exists on no island, perhaps because it gives a poor match to actual production curves, as suggested by this figure if the actual consumption curves are similar to the production curve.

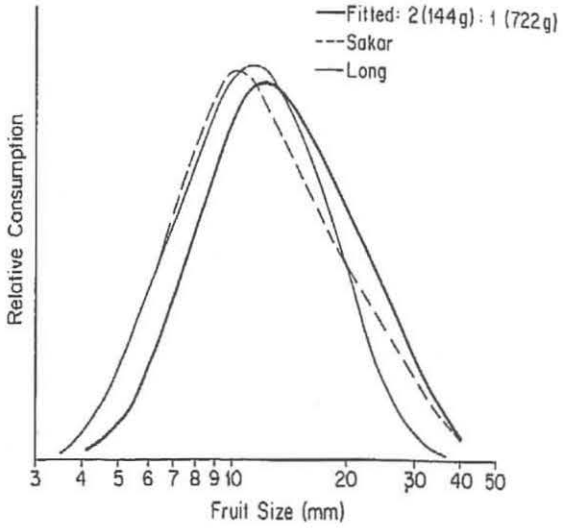


Figure 48 Like Figure 47, except that the fitted curve is for the imaginary combination *P. insolitus* (144 g) and *D. rubricera* (722 g), with abundances adjusted to the ratio 2:1. The imaginary combination consumes less small fruit and more medium-sized or large fruit than the actual guilds. This combination does not exist in nature.

combination also exists on no Bismarck island. On both Sakar and Long the absence of a small pigeon in the imaginary combination would result in an unutilized production of small fruit and an excess consumption of medium or large fruit. Some other forbidden combinations, such as *P. solomonensis* + *P. insolitus* or *D. pistrinaria* + *D. rubricera,* yield much worse best-fit curves.

Thus, if the actual consumption curves for Sakar and Long are similar to the production curves, the reason for the nonexistence of so-called forbidden combinations could be that they give too poor a fit to the production curves of real islands. Without knowledge of the actual production curves, we cannot decide whether the actual species combination on Long could equally well be on Sakar and vice versa, and whether these two islands support different combinations for fortuitous reasons; or whether there are slight differences in the production curves that selected for different successful combinations on the two islands (see discussion of "Chance or predestination?" in the final section of this chapter).

Figures 47 and 48 obviously represent only a preliminary attempt to understand assembly rules in terms of matches between consumption curves and production curves. Some of the technical problems that will have to be overcome in a more detailed analysis include the following: 1. The shape of the production curve must be measured directly. 2. Absolute values must be obtained both for production and for consumption. The consumption curves of Figures 47 and 48 are relative; I estimated ratios of species abundances, not absolute densities in birds per acre. 3. My measurements so far show that, for a given species, there is far less variation between islands or habitats in the fruit consumption curve (vertical cross-sections through the checkerboards of Figure 45, or curves as in Figure 31 below) than in the habitat distribution (horizontal cross-sections through the checkerboards of Figure 45, or figures such as Figure 41) or than in abundance. However, careful comparisons of single-species consumption curves in different habitats or islands are necessary, as a consumption curve could shift with a shift in the available resource curve caused by a change either in the competing species pool or in the production curve. 4. The contribution of species segregation by perch position (see Figure 30 legend) to segregation based on body size requires quantitation. I have quantitated only the contribution of segregation by fruit size, so far. 5. An analysis needs to be done at different seasons. It is possible that the shape of the production curve varies seasonally, and that a species combination that fits poorly at one season may nevertheless be preferred because of a superior fit for the rest of the year.

Companions in starvation: a mechanism of coadjustment?

The preceding discussion of utilization functions fails to explain why certain species or combinations of species are preferred over others with similar U's in the same habitat. For instance, distributions of fruit sizes eaten by supertramp fruit pigeons seem similar to those of other pigeons of comparable body size. How are supertramps normally excluded by other species?

The high population densities on supertramp-rich island or habitats (Figure 18) suggest that lowering of resource levels to mutually acceptable levels by members of successful combinations could be an important mechanism of coadjustment and exclusion. Among the incidence categories, supertramps may be most prone to starve in times of scarcity, and high-S species least. Figure 49 illustrates how this hypothetical coadjustment by resource level might operate. In simplified form, one hypothesizes an equilibrium on a medium-sized island, such that at a given time some high-S species are absent because of low K's, too few hot spots, too low reproductive potential and recolonization frequency, etc., and some super-

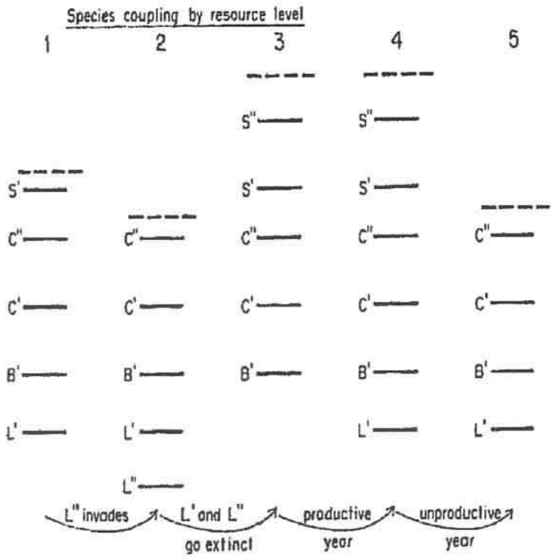
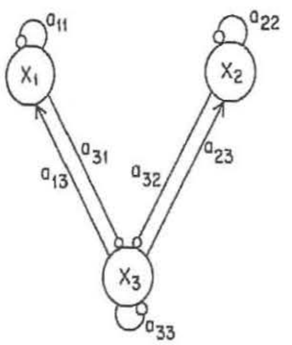


Figure 49 Hypothetical example of how occurrences of species in a community might be coupled by resource level. Members of the total species pool differ in their ability to survive at low resource levels, and also in their tendency to depress resource levels by overexploitation: the worst overexploiters can tolerate the lowest levels. A guild of species exploiting similar resources consists of supertramps S'' and S', C-tramps C'' and C', B-tramp B', and high-S species L' and L'', whose tolerance of low resource levels and tendency to overexploit increases in that sequence. For the same community in each of five states, solid bars give, for each guild member present, the lowest resource level it can tolerate (assumed invariant with community state), and the dashed bars give the actual resource level. Any species whose solid bar lies above the dashed bar is eliminated. Initially (state 1, left), species S', C'', C', B', and L' are present. A successful invasion by the worst overexploiter, L'', lowers the resource level, eliminating the species present that requires the highest resource level, S' (state 2). The overexploiters L'' and L' both go extinct owing to population fluctuations, relieving overexploitation, letting the resource level rise above the initial value, and permitting both S' and S'' to invade (state 3). An unusually productive year permits L' to invade again without lowering the resource level or eliminating species (state 4). A drought or unproductive year then lowers the resource level, eliminating S'' and S' (state 5). Among the respects in which the figure is an oversimplification is that the dashed bar lying above the solid bar of a species permits but does not guarantee its presence (e.g., the drought might also have eliminated L', and the productive year might have permitted invasion by some species B'' of intermediate tolerance between B' and C'). If this were not true, all permitted species combinations could be formulated as groups of consecutive species in a single list, which is not the case (cf. permitted combinations of cuckoo-doves, gleaning flycatchers, etc.). The figure may apply either to a whole island, or to individual habitats on an island.

tramps are starved out because the remaining species overharvest the resources to a point that these remaining species but not the supertramps can tolerate. Fluctuations in resource levels, and corresponding fluctuations among permitted species combinations, occur around this equilibrium state. Occasionally, another high-S species temporarily establishes itself or there is an unproductive year, in either case lowering the resource level. Then another supertramp is starved completely off the island, and some tramp is starved out of forest into a less stable habitat. Occasionally, there is an especially productive year, or a high-S species temporarily disappears, letting the resource level rise again. Then another supertramp is able temporarily to colonize, and an established tramp temporarily shifts back into the forest.

The plausibility and internal consistency of this proposed mechanism of resource coupling may be assessed by means of loop analysis, the technique used by Levins in Chapter 1 for studying evolution in communities near equilibrium. The treatment in this and the next paragraphs is based on Levins's formulation of loop analysis, which may be consulted for an explanation of loops, feedback, stability conditions, and methods for determining effects of selection for a particular trait on the equilibrium abundance of the species in a community. Figure 50 represents the simplest possible system that could exhibit resource coupling and competitive exclusion by overexploitation. The system consists of two species (X_1 and X_2) that harvest the same nutrient (X_3). The coeffi-



$$\begin{bmatrix} -a_{11} & 0 & a_{13} \\ 0 & -a_{22} & a_{23} \\ -a_{31} & -a_{32} & -a_{33} \end{bmatrix}$$

Figure 50 Left: loop diagram of a three-variable community consisting of two species X_1 and X_2 harvesting the same nutrient X_3. See Levins, Chapter 1, for explanation of loop diagrams. The coefficients a_{ij} represent the effect of species j on the growth of species i in the equation $dX_i/dt = f_i(X_i, X_j)$, where $a_{ij} \equiv \partial f_i/\partial X_j$. On the right is the community matrix for this system, taking all the a_{ij} as positive numbers and representing the directions of their effects by the sign in front. See text for discussion.

cients a_{ij} in the growth equation (Levins, Chapter 1, eq. 1)

$$dX_i/dt = f_i(X_1, X_2, X_3)$$

are defined by

$$a_{ij} \equiv \partial f_i/\partial X_j$$

For example,

$$dX_3/dt = f_3(X_1, X_2, X_3)$$
$$a_{31} \equiv \partial f_3/\partial X_1$$

Thus, the coefficients a_{31} and a_{32}, which represent the effects of X_1 and X_2 on the growth of X_3 in the growth equation for dX_3/dt, are negative; and the coefficients a_{13} and a_{23}, which represent the effect of X_3 on the growth of X_1 and X_2, respectively, are positive. The growth of X_3 will in general either be self-damped or will incorporate the damping effect of non-self-reproducing resources at a lower trophic level that are not otherwise represented in Figure 50. Thus a_{33}, the effect of X_3 on its own growth, is negative. The growths of X_1 and/or X_2 may or may not be self-damped (a_{11}, a_{22} negative?). We ask the question: under what conditions is an overexploitation strategy profitable for its practitioner? That is, suppose one of the consumer species, X_1, evolves a trait C that tends to let the species grow faster but tends to deplete nutrient ($\partial f_1/\partial C > 0$, $\partial f_3/\partial C < 0$, $\partial f_2/\partial C = 0$). Under what conditions can this species thereby eliminate the other consumer species without also eliminating itself?

First, we write the expressions for feedback F_1, F_2, and F_3 at all three levels in the system, to determine stability conditions. From eqs. 8–10 of Levins, Chapter 1, these expressions become:

$$F_1 = (-a_{11}) + (-a_{22}) + (-a_{33}) \qquad (9)$$

$$\begin{aligned} F_2 = {} & (a_{13})(-a_{31}) + (a_{23})(-a_{32}) \\ & - (-a_{11})(-a_{22}) - (-a_{11})(-a_{33}) \\ & - (-a_{22})(-a_{33}) \qquad (10) \end{aligned}$$

$$\begin{aligned} F_3 = {} & (-a_{11})(-a_{22})(-a_{33}) \\ & - (-a_{11})(a_{23})(-a_{32}) \\ & - (-a_{22})(a_{13})(-a_{31}) \qquad (11) \end{aligned}$$

(In eqs. 9–11, in the following analysis, and in the right side of Figure 50 we take all a_{ij} as positive numbers and indicate their effect on dX_i/dt by the sign). One stability condition is that feedback at all levels be negative. This will be true of F_1 and F_2 whether or not a_{11} and/or a_{22} are zero, but if both a_{11} and a_{22} are zero, F_3 is zero and the system is unstable. Thus, one or both of the consumer species must be self-damped for the two species to coexist. The other stability condition (eq. 27 of Levins, Chapter 1) is that $F_1F_2 + F_3$ must be positive. Expressing $F_1F_2 + F_3$ in terms of eqs. 9–11 yields 12 positive terms if a_{11} and a_{22} are both negative; two of these terms remain if $a_{11} = a_{22} = 0$. Thus, this condition imposes no new restraints.

The effect of natural selection for the trait C on the abundance of the species X_i is obtained by replacing column i of the community matrix (Figure 50) with the vector

$$\begin{bmatrix} -\partial f_1/\partial C \\ 0 \\ +\partial f_3/\partial C \end{bmatrix}$$

and dividing by F_3, $\partial f_1/\partial C$ and $\partial f_3/\partial C$ both being positive quantities. This yields:

$$\frac{\partial X_1}{\partial C} = \frac{\begin{vmatrix} -\partial f_1/\partial C & 0 & a_{13} \\ 0 & -a_{22} & a_{23} \\ \partial f_3/\partial C & -a_{32} & -a_{33} \end{vmatrix}}{F_3}$$

$$= \frac{[(\partial f_1/\partial C)a_{22}a_{33} + (\partial f_1/\partial C)a_{23}a_{32} - (\partial f_3/\partial C)a_{13}a_{22}]}{a_{11}a_{22}a_{33} + a_{11}a_{23}a_{32} + a_{22}a_{13}a_{31}} \quad (12)$$

$$\frac{\partial X_2}{\partial C} = \frac{\begin{vmatrix} -a_{11} & -\partial f_1/\partial C & a_{13} \\ 0 & 0 & a_{23} \\ -a_{31} & \partial f_3/\partial C & -a_{33} \end{vmatrix}}{F_3}$$

$$= \frac{[-(\partial f_3/\partial C)a_{11}a_{23} - (\partial f_1/\partial C)a_{23}a_{31}]}{a_{11}a_{22}a_{33} + a_{11}a_{23}a_{32} + a_{22}a_{13}a_{31}} \quad (13)$$

$$\frac{\partial X_3}{\partial C} = \frac{\begin{vmatrix} -a_{11} & 0 & -\partial f_1/\partial C \\ 0 & -a_{22} & 0 \\ -a_{31} & -a_{32} & \partial f_3/\partial C \end{vmatrix}}{F_3}$$

$$= \frac{[-(\partial f_3/\partial C)a_{11}a_{22} - (\partial f_1/\partial C)a_{22}a_{31}]}{a_{11}a_{22}a_{33} + a_{11}a_{23}a_{32} + a_{22}a_{13}a_{31}} \quad (14)$$

Since $\partial f_1/\partial C$, $\partial f_3/\partial C$, and all the a_{ij} in eqs. 12–14 are positive quantities, $\partial X_2/\partial C$ and $\partial X_3/\partial C$ are always negative, whereas $\partial X_1/\partial C$ may be either positive or negative (two of the terms make it positive, one makes it negative). Thus, selection in X_1 for increase at the expense of nutrients always decreases the abundance of the competitor X_2 and the nutrient X_3, but the direction of the effect on the abundance of X_1 itself depends on the values of the system parameters.

Examining the effects of individual parameters in eqs. 12–14, we draw five further conclusions:

If $a_{22} = 0$, then $\partial X_1/\partial C$ consists only of one positive term, and $\partial X_3/\partial C = 0$. Furthermore, the denominator of eqs. 12–14 loses two of its three terms, increasing the damage to X_2's abundance and the stimulation to X_1's abundance. That is, if the competitor does not self-regulate his growth at all, the evolving consumer is guaranteed to increase his own abundance and harm his competitor without even lowering the nutrient level. In effect, the species undergoing selection simply diverts to his own use some resources that would previously have gone to his unregulated rival.

Conversely, large a_{11} (X_1 highly self-damped) hurts X_2 more than X_1, since a_{11} terms appear in the denominator for both $\partial X_1/\partial C$ and $\partial X_2/\partial C$ but only in the numerator, as a negative term, in $\partial X_2/\partial C$.

If a_{23} is large, the rival is hurt greatly, since a_{23} appears in both terms of $\partial X_2/\partial C$; and the evolving species is more likely to increase his own abundance, since a_{23} appears in a positive term of $\partial X_1/\partial C$. If a_{13} is small, the evolving species is less likely to decrease in abundance, since a_{13} appears in a negative term of $\partial X_1/\partial C$. The greater the inequality $a_{13} < a_{23}$, the more valuable does the trait C become. To interpret the meaning of this inequality, recall that a_{i3} gives the magnitude of the effect of changes in nutrient level on the growth of the species X_i. Thus, a species that can increase very rapidly under conditions of abundance but that survives very poorly under conditions of scarcity will be particularly hard hit if a competitor evolves to overexploit. Conversely, a species that at best increases slowly but that also weathers bad times well can afford to overexploit: depletion of nutrient will differentially affect the rival's population.

A large a_{32}, by contributing to a positive term of $\partial X_1/\partial C$, tends to make X_1 increase rather than decrease in abundance. Large a_{32} would mean that the rival initially harvests much of the resources, so that the evolving species has much to gain by preempting the rival's share.

Finally, large $(\partial f_1/\partial C)$ contributes to two positive terms in $\partial X_1/\partial C$ and one negative term in $\partial X_2/\partial C$. Even if large $(\partial f_1/\partial C)$ inevitably means large $(\partial f_3/\partial C)$ for biological reasons (growth of X_1 achieved at the expense of nutrient depletion), the $(\partial f_1/\partial C)$ and $(\partial f_3/\partial C)$ terms both act to depress X_2 but tend to cancel in their effects on X_1 because of opposite signs.

We can summarize by saying that overexploitation is a viable strategy for a species faced with competitors; and that it is an especially profitable strategy for a species that regulates its own population closely and has low reproductive potential but good ability to survive scarcity, when the species is confronted with a rival that has high reproductive potential, breeds without limit, squanders resources, and crashes in times of scarcity. By overexploiting, the former species can decrease its rival's abundance more than its own, and may even increase its own abundance. But this description of the rival matches exactly with the properties of supertramps and *r*-selected species, whereas the successful overexploiter matches the description of a *K*-selected species. Thus, as one proceeds through the incidence categories from high-*S* species to supertramps, one passes down a hierarchy from plausible practitioners to plausible victims of overexploitation. The striking abundance of bird individuals in supertramp-dominated islands or habitats (Figure 18) is consistent with this interpretation of resource coupling derived from loop analysis and depicted in Figure 49.

Dispersal and Assembly

We have so far discussed assembly rules as if they were determined solely by how species utilize resources. This is obviously not the full explanation, else supertramps would be starved out everywhere. In fact, on a small island no population survives long. Among two competing species of mutually exclusive requirements, an equilibrium is established on a small island, such that the fraction of time each species is present depends not only on competitive ability (or resource utilization) but also on population size and interisland dispersal rate. As discussed by Levins and Culver (1971) and Horn and MacArthur (1972), a species with a sufficiently high dispersal rate may thereby occupy the island for more of the time than does the species with superior competitive ability. Overexploitation, by reducing population size, becomes a dangerous strategy on a small island. Thus the supertramps, with their twin advantages of high dispersal rates and large populations, are increasingly favored on islands of decreasing size. The species of small islands will be to some extent the species that share these advantages.

Transition Probabilities

It is conceivable that certain species combinations that would be superior in utilization of resources may not exist in nature because it is too difficult to assemble them from other permitted combinations. For instance, suppose that a certain four-species combination could be assembled from permitted three-species combinations only by eliminating two of the species and adding three others; and could be assembled from permitted five-species combinations only by eliminating three species and adding two others. Since such changes are much less likely to occur simultaneously than is the addition or subtraction of a single species, and since the intermediate combinations would be forbidden, such a four-species combination might never be assembled because of low transition probabilities.

To assess the significance of this consideration, let us compare the ease of assembly of the permitted and forbidden combinations in the guilds we have discussed:

Among the cuckoo-doves (Table 7), all permitted combinations of *n* species, $p.c._n$, can be assembled from below (i.e., from $p.c._{n-1}$) by addition of a single species (e.g., $AR + N \rightarrow ANR$). One of the $p.c._2$ and both of the $p.c._1$ can be assembled from above (from $p.c._{n+1}$) by loss of a single species (e.g., $AR - R \rightarrow A$), but two of the $p.c._2$ (*AM* and *MR*) cannot. Of the forbidden combinations of *n* species ($f.c._n$), five (*R, AN, AMN, AMR, MNR*) can be assembled in a single step from below or above, three (*N, MN, AMNR*) from below but not from above, and one (*NR*) from above but not from below.

Among the gleaning flycatchers, nine *p.c.*'s can be assembled in one step from above or below, five just from below, one just from above (*APV* on Umboi, probably derived by loss of *H* from *AHPV* on New Britain, formerly in near-contact with or joined by a land-bridge to Umboi), and two (*CHPV* and *ACDH,* on one island each) in neither direction. These last two combinations could have been derived either by addition of two species to a $p.c._2$, by addition of two species and loss of one species in a $p.c._3$, by replacement of one species in a $p.c._4$, or by two-for-one (*CHPV*) or three-for-two (*ACDH*) substitution in the sole $p.c._5$, *AHPRV*. *ACDV* on the land-bridge island Duke of York was probably in fact assembled by loss of *HP* from the parent New Britain combination *AHPV* and immediate colonization by the supertramps *C* and *D*. On St. Matthias *CHPV*, which includes the supertramp *C*, could have been assembled in several plausible ways (e.g., $AHPV - A + C$, $APV + H - A + C$). Among the $f.c._2$ and $f.c._3$, 13 can be assembled in one step from above or below, 11 from below but not from above, 9 from above but not from below, and 15 from neither direction. None of these forbidden combinations would require more steps to assemble than the permitted combinations *CHPV* and *ACDH*. The myzomelid-sunbird guild yields a qualitatively similar picture.

Thus, most permitted combinations can be assembled in one step, although a few require more numerous but still plausible transition steps. Simultaneous invasions by several species in a guild may occur if the species are all stimulated by the same environmental change to send out immigrants. For instance, Meyer (1906) recorded an invasion of Vuatom, then inhabited by the fruit pigeons *Ducula rubicera* and *D. pistrinaria*, by mixed flocks of *Ducula melanochroa*, *D. finschii*, and *D. spilorrhoa;* the invaders disappeared, leaving the original two species, one of which then disappeared during the next few decades. On Umboi invasions of both *Ptilinopus superbus* and *P. solomonensis* within a few decades virtually supplanted *P. solomonensis*. Near-simultaneous extinctions of several species may occur if the extinction of one species of a $p.c._n$ yields a $f.c._{n-1}$ and another species is then rapidly expelled to reach a $p.c._{n-2}$. Thus, relaxation of guilds on land-bridge islands could proceed in steps. (cf. p. 411).

Conversely, most but not all forbidden combinations can be assembled in one step. Whether low transition probabilities are the explanation for a few forbidden combinations remains uncertain.

Summarizing our discussion of the origin of assembly rules, we conclude that resource utilization must be a major factor. Permitted combinations may leave fewer resources unutilized than forbidden combinations with the same total number of species. In addition, the various species of a permitted combination must be "companions in starvation," i.e., must have roughly comparable abilities to tolerate lowered resource levels. On increasingly small or remote islands, the ability to arrive frequently and maintain a large population becomes an increasingly significant consideration in determining what species will co-occur. Finally, the possibility exists that some combinations are just difficult to assemble, especially if some of their component species colonize infrequently.

Unsolved Problems

The finding that community assembly obeys the rules discussed above raises numerous unsolved problems of interpretation, some of which will be briefly summarized.

Reconstructing incidence functions.

The incidence function of a species is expected to depend on the species' territory size, population density, birth and death rates, and dispersal rates; on similar properties of competing species; and on island area and isolation. It should be feasible to develop mathematical models of incidence functions, initially for guilds of a few species.

Applications to habitat communities, and to locally patchy communities.

The incidence functions of Figures 4–15, 19, 25, 28, and 29 were all constructed for communities each of which corresponds to a single island. Such functions were feasible to construct because islands are the easiest communities to delimit, hence species lists (the starting point for construction of incidence functions) were available for many Bismarck islands. Correspondingly, the discussion of assembly rules on pp. 393–411 was based on island communities. However, the discussions of pp. 412–416 and of pp. 416–423 suggest that assembly rules exist, and incidence functions can be profitably constructed, for communities corresponding to local geographical areas, and for communities corresponding to single habitats. Applied to local geographical areas, this approach may help rationalize the phenomenon of tropical patchiness resulting from diffuse competition. Applied to habitat communities, the approach may permit prediction of expansion and compression in habitat preference associated with changes in diffuse competition. The main practical problem may be to obtain enough good local lists for a tropical area with patchy distributions, or enough islands with good information about variation in species habitat preference. In addition, the abundance of a species often varies with competition from other species (see discussions of "density compensation" by Crowell, 1962; Diamond, 1970a, 1970b; MacArthur et al., 1972; Cody, Chapter 10; Brown, Chapter 13). Where competition is diffuse, it may prove profitable to plot abundance as a function of the number of competing species (cf. Yeaton and Cody, 1974, Fig. 1); such curves may have the form of incidence functions inverted.

Chance or predestination?

At the one extreme, the species composition of an island fauna might be uniquely determined by an island's physical properties. Combinations of colonists might be reshuffled through invasion and extinction until the best-suited groups of colonists had been assembled, and these would then persist. (This view is surely valid if applied to supertramp exclusion from large islands.) Differences between the faunas of apparently similar islands might really be due to slight physical differences in the islands selecting those combinations of colonists that had a slight selective advantage. For instance, the consumption curve for the fruit-pigeon guild shows a slight proportionate excess of large fruits on Sakar compared with Long (Figure 46). If this same finding applied to the fruit production curves, it might help explain why Sakar supports the pigeon combination *Ptilinopus solo-*

monensis (91 g), *P. insolitus* (144 g) and *Ducula rubricera* (722 g), whereas the Long lowlands support the combination *Ptilinopus solomonensis* (91 g) and *Ducula pistrinaria* (470 g): the greater abundance of large fruits on Sakar would favor the very large *D. rubricera* over the medium-large *D. pistrinaria,* leaving a gap between the *Ducula* and the very small *P. solomonensis* into which the medium-small *P. insolitus* could fit. At present such reasoning would be totally circular, since the production curves are unknown. Such detailed differences in production curves would be hard to detect or measure but could be very important.

At the other extreme, chance in the form of random historical events might play a large role in building up nonidentical communities that represent alternative stable equilibria. Of several closely related species, whichever happens to arrive first may become so numerous by the time a competitor arrives that it may be impossibly difficult for the later arrival to establish itself. Or, selection of the first successful colonist within a group of related species may then prejudice the chances of success among the remaining species, some of which will "fit" better than others with the first arrival. Any given community would thus represent one out of many possible, alternative, stable communities, drawn in turn from a much larger number of less stable communities that could be constructed on paper from the same species pool.

Numerous findings suggest at least some role of chance. After all, there does occur turnover in species compositions of islands that are at equilibrium with respect to species number, so that species composition wanders among adjacent stability maxima. Often, a habitat that suddenly becomes available may be colonized by whatever species is experiencing a "bloom" in the vicinity at that time (Connell, Chapter 16). For instance, the incidence of the supertramp *Zosterops griseotincta* (known from no Bismarck volcano except Long and its two neighbors) is so low that its colonization of Long after the explosion seems much more likely to have been the product of a bloom at the right time than of a uniquely good fit to local conditions. Yet this supertramp is now the most abundant and ubiquitous bird of Long, is omnivorous, must have severely restricted the selection of what other small bird species could colonize Long, and thereby played a key role in the assembly of the present Long community. Similarly, each of the eight *Lonchura* grass finches that have distributed themselves checkerboard-fashion in the New Guinea midmontane grasslands (Figure 33) occupies a wide range of altitudes, rainfall conditions, and grassland types. This suggests that the locally successful colonist was selected on a first-come first-served basis rather than because of locally superior attributes.

The problem of chance vs. predestination is still more acute for plants. Among plants that seed at long intervals, happening to seed at the right time may be even more important to success in colonizing suddenly vacant habitats, than among birds. If the first-arriving plant grows a foot tall before the seeds of an ultimately superior competitor arrive, and if in addition the first arrival is profusely self-replacing, the competitor may be kept out for a long time (cf. Horn, Chapter 9). Plant communities may also be much more closely integrated and resistant to invaders than bird communities, as suggested by such biogeographic chimaeras as the old island of New Caledonia, which supports an old endemic flora but an avifauna composed mostly of recent arrivals.

Applications to conservation problems.

Recently, there has been increasing recognition of the potential practical contributions that the theory of island biogeography may make to a rational design of nature preserves (Willis, 1974; Diamond, 1972b, 1975; Terborgh, 1974a, 1974b; Wilson and Willis, Chapter 18) A piece of threatened habitat, set aside for conservation purposes, becomes a distributional island for species tied to that habitat. The number of species in a refuge is expected to be a function of refuge area. In addition, the incidence functions of Figures 4-15 show that species composition will be a function of refuge area. A refuge of a size capable of holding a certain species number S_i at equilibrium will eventually lose all species whose lower S_{crit} values exceed S_i, and will lose half of the species for which $J(S_i) = 0.5$. This could be a serious problem, because high-S species include a disproportionate fraction of an island's endemic forms and may be especially in need of protection.

An example is provided by the fourth-largest Bismarck island, New Hanover, which was joined by a land bridge to the second-largest Bismarck island, New Ireland, during the Pleistocene. At that time New Hanover must have shared most of New Ireland's species. Today, New Hanover has lost 23 New Ireland species but still has a total of 81 species and is still somewhat supersaturated for its area. A loss of 23 species, or about 22% of the original number, does not seem serious. However, among these lost species, New Hanover lost 19 of the 26 high-S species of New Ireland, including every one of the 5 New Ireland high-S species that are endemic to the Bismarcks at the species level. As a faunal preserve, New Hanover would rate as a disaster. Yet its area of 458 square miles is not small by the standards of many of the tropical rainforest parks that one can realistically hope for today.

The incidence function of a species that becomes threatened may be useful in suggesting the minimum area of a refuge that would be adequate to ensure its survival (i.e., to have a high J for that species). In addition, assembly rules may suggest what combinations of guild relatives can share a refuge with a species requiring protection, and not threaten its survival.

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